



# Quaestiones Entomologicae

---

**A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.**

## CONTENTS

Darling—A Review of the New World Species of <i>Euperilampus</i> (Hymenoptera: Chalcidoidea), with Notes about Host Associations and Phylogenetic Relationships . . . . .	1
Lacey and Lacey—Filter Feeding of <i>Simulium fulvinotum</i> (Diptera: Simuliidae) in the Central Amazon Basin . . . . .	41
Fredeen—Trends in Numbers of Aquatic Invertebrates in a Large Canadian River during Four Years of Black Fly Larviciding with Methoxychlor (Diptera: Simuliidae) . . . . .	53
Ball and Hilchie—Cymindine Lebiini of Authors: Redefinition and Reclassification of Genera (Coleoptera: Carabidae) . . . . .	93
Book Review—Malicky, H. 1983. Atlas of European Trichoptera . . . . .	217
Goulet—The Genera of Holarctic Elaphrini and Species of <i>Elaphrus</i> Fabricius (Coleoptera: Carabidae); Classification, Phylogeny and Zoogeography . . . . .	219
Book Review—Chvála, M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families of Hybotidae, Atelestidae and Microphoridae. . . . .	483
Book Review—Duval, C. T. (Series Editor). 1982. Fauna of New Zealand. . . . .	486
Book Review—Griffiths, G. C. D. (Editor). 1982. Flies of the Nearctic Region. . . . .	489
Book Review—Halffter, G. and W. D. Edmonds. 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae)—an Ecological and Evolutive Approach . . . . .	491
Editor's Acknowledgements . . . . .	494
Index to Volume 19 . . . . .	495



**Ball, G. E. and G. J. Hilchie (1983, 19: 93–216).– Cymindine Lebiini of Authors: Redefinition and Reclassification of Genera (Coleoptera: Carabidae).**

### CORRIGENDA

#### pages

93 Title

“Coleoptera” was misspelled in the title. The corrected title is :CYMINDINE LEBIINI OF AUTHORS: REDEFINITION AND RECLASSIFICATION OF GENERA (COLEOPTERA: CARABIDAE).

### ADDENDA

#### 204 ACKNOWLEDGEMENTS

Financial support for this study was received through Grant A- 1399, Natural Sciences and Engineering Research Council of Canada. Funds for publication were received through Grant A- 1399 and through a grant from the Central Research Fund (NSERC), University of Alberta. The authors very much appreciate this assistance.



Q L  
461  
Q13  
Ent.

# Quaestiones

# Entomologicae



**A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.**





A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

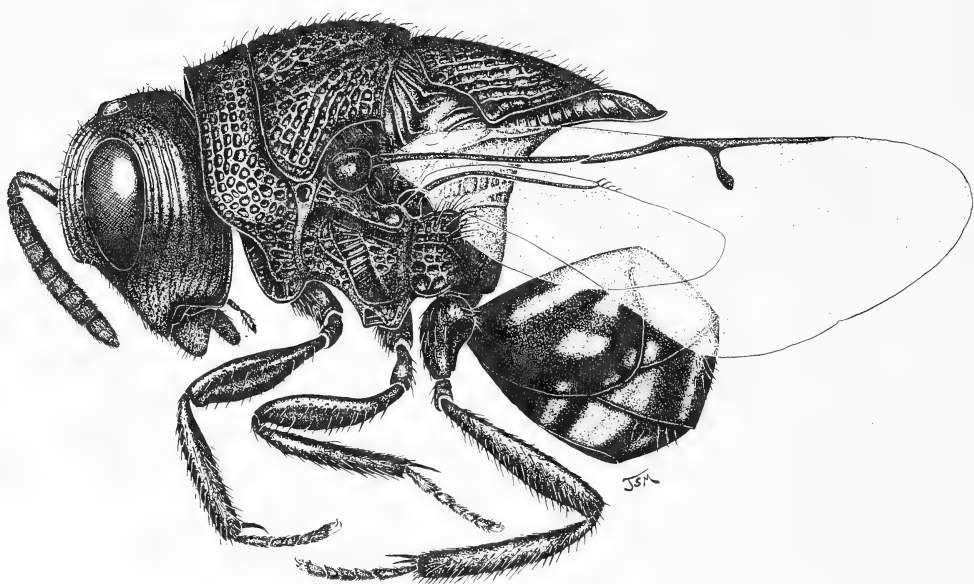
Volume 19

Numbers 1-2

1983

# CONTENTS

Darling—A Review of the New World Species of <i>Euperilampus</i> (Hymenoptera: Chalcidoidea), with Notes about Host Associations and Phylogenetic Relationships . . . . .	1
Lacey and Lacey—Filter Feeding of <i>Simulium fulvinotum</i> (Diptera: Simuliidae) in the Central Amazon Basin . . . . .	41
Fredeen—Trends in Numbers of Aquatic Invertebrates in a Large Canadian River during Four Years of Black Fly Larviciding with Methoxychlor (Diptera: Simuliidae) . . . . .	53
Ball and Hilchie—Cymindine Lebiini of Authors: Redefinition and Reclassification of Genera (Coleoptera: Carabidae) . . . . .	93
Book Review—Malicky, H. 1983. Atlas of European Trichoptera . . . . .	217



*Euperilampus triangularis* Say, female

A REVIEW OF THE NEW WORLD SPECIES OF *EUPERILAMPUS* (HYMENOPTERA;  
CHALCIDOIDEA), WITH NOTES ABOUT HOST ASSOCIATIONS AND  
PHYLOGENETIC RELATIONSHIPS.

D. Christopher Darling  
Entomology  
Cornell University  
Ithaca, New York  
14853

*Quaestiones Entomologicae*  
19: 1-40 1983

ABSTRACT

The genera *Perilampus* Latreille, *Euperilampus* Walker, *Krombeinius* Bouček, *Steffanolampus* Peck, and *Monacon* Waterston form a monophyletic taxon ranked either as a family (*Perilampidae*), or as a subfamily (*Perilampinae*) of the *Pteromalidae*. Based on synapomorphic character states of size of postspiracular sclerite, pronotal size, and sculpture of inner orbits and propodeum, *Krombeinius* Bouček and *Euperilampus* Walker are sister groups, their common ancestor in turn being the derived sister group of the *Perilampus hyalinus* species group. The subgenera *Euperilampus* sensu stricto (type species *Perilampus gloriosus* Walker, 1862) and *Euperilampoides* Girault (type species *Euperilampoides scutellatus* Girault, 1915) are invalid taxa in a phylogenetic system, because character states hypothesized to be synapomorphic for them are more likely homoplasious. The 12 New World species of *Euperilampus* are arranged in three groups: the *E. tanyglossa* group; *E. krombeini* Burks; and the *E. triangularis* group. The *E. tanyglossa* group includes two Mexican species, *E. tanyglossa* new species (type locality—Jalisco, Zapotlanejo), and *E. aureicornis*, new species (type locality—Guerrero, Amula). The sister group of these species is hypothesized to be the Old World species *E. mediterraneus* Bouček, and to be related to *E. scutellatus* Girault, 1915, another Palearctic species. The *E. tanyglossa* group + *E. mediterraneus* + *E. scutellatus*, based on synapomorphic features of notauli and mesoscutal sculpture, comprise the sister group of the stem of *E. krombeini* + the *E. triangularis* group. The latter is based on synapomorphic features of postspiracular sclerite, propodeal and mesoscutal sculpture, and color of body and wings, and includes nine New World species, of which four are in the *E. brasiliensis* complex, and the others are not further classified. Members of the *E. brasiliensis* complex are: *E. brasiliensis* (Ashmead); *E. enigma*, new species (type locality—Bolivia, Santa Cruz, Roboré); *E. ameca*, new species (type locality—México, Nayarit, Santa Isabel); and *E. luteicrus* (type locality—México, Jalisco, Guadalajara). The unclassified species of the *E. triangularis* group are *E. triangularis* (Say); *E. gloriosus* (Walker); *E. magnus*, new species (type locality—México, Chiapas, El Chorreadero); *E. solox*, new species (type locality—Argentina, Tucuman, Tacanas); and *E. iodes*, new species (type locality—Brazil, Santa Catarina, Nova Teutonia). Because of a shortage of reliably interpretable characters, a reconstructed phylogeny of the species of the *E. triangularis* group is not proposed. *Euperilampus triangularis* is a parasitoid of the ichneumonid, *Hyposoter fugitivus* Say, itself a parasitoid of the arctiid, *Hyphantria cunea* (Drury).

## RÉSUMÉ

Les genres *Perilampus* Latreille, *Euperilampus* Walker, *Krombeinius* Bouček, *Burksilampus* Bouček, *Steffanolampus* Peck, et *Monacon* Waterston constituent une lignée monophylétique classifiée soit comme famille (*Perilampidae*), ou comme une sous-famille (*Perilampinae*) des *Pteromalidae*. En considérant les conditions synapomorphiques de la taille du sclérite postspiraculaire et du pronotum, et de la sculpture de la région intraorbitale et du propodéum, *Krombeinius*; *Bouček* et *Euperilampus* Walker représentent des taxons frères, dont l'ancêtre commun est à son tour le taxon dérivé et frère du groupe d'espèces de *Perilampus* hyalinus. Les sous-genres *Euperilampus* sensu stricto (espèce type: *Perilampus gloriosus* Walker, 1862) et *Euperilampoides* Girault (espèce type: *Euperilampoides scutellatus* Girault, 1915) sont des taxons invalides dans le cadre d'une classification phylogénétique, parce que les conditions des caractères supposément synapomorphiques regroupant les deux sont probablement issues de convergence. Les 12 espèces d'*Euperilampus* du Nouveau Monde sont arrangées en trois groupes: le groupe d'*E. tanyglossa*; *E. krombeini* Burks; et le groupe d'*E. triangularis*. Le groupe d'*E. tanyglossa* comprend deux espèces mexicaines: *E. tanyglossa*, nouvelle espèce (localité du type: Jalisco, Zapotlanejo), et *E. aureicornis*, nouvelle espèce (localité du type: Guerrero, Amula). Le taxon frère de ces espèces est supposé être *E. mediterraneus* Bouček, de l'Ancien Monde, et serait lui-même apparenté à *E. scutellatus* Girault, 1915, une autre espèce eurasiennne. Basé sur les particularités synapomorphiques des notauli et de la sculpture du mésoscutum, le groupe d'*E. tanyglossa* forme, avec les espèces *E. mediterraneus* et *E. scutellatus*, le taxon frère d'*E. krombeini* et du groupe d'*E. triangularis*. Ce dernier est défini à partir de caractéristiques synapomorphiques du sclérite postspiraculaire, de la sculpture du propodéum et du mésoscutum, et de la couleur du corps et des ailes; il comprend neuf espèces du Nouveau Monde, parmi lesquelles quatre font partie du complexe d'*E. brasiliensis*, tandis que les autres ne sont pas classifiées. Les membres du complexe d'*E. brasiliensis* sont: *E. brasiliensis* (Ashmead); *E. enigma*, nouvelle espèce (localité du type: Bolivie, Santa Cruz, Roboré); *E. ameca*, nouvelle espèce (localité du type: Mexique, Nayarit, Santa Isabel); et *E. luteicrus*, nouvelle espèce (localité du type: Mexique, Jalisco, Guadalajara). Les espèces non classifiées du groupe d'*E. triangularis* sont: *E. triangularis* (Say); *E. gloriosus* (Walker); *E. magnus*, nouvelle espèce (localité du type: Mexique, Chiapas, El Chorradero); *E. solox*, nouvelle espèce (localité du type: Argentine, Tucuman, Tacanas); et *E. iodes*, nouvelle espèce (localité du type: Brésil, Santa Catarina, Nova Teutonia). L'auteur ne présente pas de diagramme phylogénétique pour les espèces du groupe d'*E. triangularis* à cause d'un manque de caractères interprétables de façon sûre. *Euperilampus triangularis* est un parasitoïde d'*Hyposoter fugitivus* Say, un *Ichneumonidae* lui-même parasitoïde de l'*Arctiidae* *Hyphantria cunea* (Drury).

## TABLE OF CONTENTS

Introduction	2
Synopsis of the New World Species of <i>Euperilampus</i>	3
Methods and Terms	3
Material	5
Key to New World <i>Euperilampus</i>	7
The New World Species of <i>Euperilampus</i>	8
Phylogenetic Relationships	34
Acknowledgements	38
Literature Cited	38

## INTRODUCTION

The genera *Perilampus* Latreille, *Euperilampus* Walker, *Krombeinius* Bouček, *Burksilampus* Bouček, *Steffanolampus* Peck and *Monacon* Waterston form a well defined monophyletic taxon regarded as either the family *Perilampidae* (Graham 1969) or as a subfamily in the *Pteromalidae*, the *Perilampinae* (sensu Bouček 1978). Bouček (1978) has characterized this taxon and reviewed the arguments concerning the placement of this group in the higher classification of the Chalcidoidea. No resolution will be possible until phylogenetic studies are conducted in the Chalcidoidea. The *Pteromalidae* is most certainly a paraphyletic group (possible polyphyletic), and relegating *Perilampus* and related genera to this unnatural assemblage is unwarranted phylogenetically and practically. I therefore follow Graham (1969)



and recognize the family Perilampidae. I exclude Chrysolampinae (sensu Graham 1969) from this family, again following Graham (1969). Larval structures of *Chrysolampus thenae* (Walker) were discussed by Askew (1980), and offer no basis for inclusion of this genus in a higher taxon with the genus *Perilampus*. Where known, all species of *Perilampus* have a planidial first instar larva (Smith 1912, Clancy 1946, Principi 1947). This type of larva is not found in *Chrysolampus*. The larval characters cited by Askew (1980) as indicating a close relationship between *Perilampus* and *Chrysolampus* are widely distributed in many chalcidoid taxa (see Parker 1924) and are here regarded as plesiomorphies.

Revisions are currently available for all genera of Perilampidae except the large cosmopolitan genus *Perilampus* (Bouček 1980, for *Monacon*; Bouček 1978, all other genera). In assembling material for a revisionary study of New World *Perilampus* I have received undescribed species of *Euperilampus* from México and South America that provide important insights into the phylogeny and biogeography of *Euperilampus*.

In this paper I discuss generic characters of *Euperilampus*, examine the validity of the current subgeneric classification, and review and present a key to the New World species. Eight new species are described, and all New World species except *E. gloriosus* are redescribed. The host associations of *E. triangularis* are also discussed. A cladogram of species groups of *Euperilampus* is presented, and the phylogenetic relationships of *Krombeinius*, *Euperilampus* and *Perilampus* are discussed.

## SYNOPSIS OF THE NEW WORLD SPECIES OF *EUPERILAMPUS*

### *E. tanyglossa* species group

*E. tanyglossa* n. sp.

*E. aureicornis* n. sp.

### *E. krombeini* Burks

### *E. triangularis* species group

*E. triangularis* (Say)

*E. gloriosus* (Walker)

*E. magnus* n. sp.

*E. solox* n. sp.

*E. iodes* n. sp.

### *E. brasiliensis* complex

*E. brasiliensis* (Ashmead) n. comb.

*E. enigma* n. sp.

*E. luteicrus* n. sp.

*E. ameca* n. sp.

## METHODS AND TERMS

*Color*.— All New World species of *Euperilampus* exhibit metallic or iridescent colors that are difficult to describe. These structural colors are the result of interference patterns, due to asynchrony between the component wavelengths of entering and returning light. The predominant color depends primarily on thickness of alternating cuticular lamellae and distance between successive lamellae and, to a lesser degree, on angle of incidence of incoming light. A change in angle of incidence from 60 degrees to 90 degrees can result in a 40 nm color

shift. This can result in changes in color from violet to blue-violet or from blue to blue-green (Fox 1979). Metallic colors can therefore only be described in general terms. I use spectral colors, i.e., violet is preferred to purple, purple being a pigmentary color resulting from a mixture of reds and blues. In this paper all colors were described when viewed under diffuse incandescent light.

Care must also be taken in describing metallic colors of specimens subjected to certain taxonomic procedures. For instance, lacto-phenol (a clearing agent) and thymol (an anti-fungicide used in relaxing jars) are swelling agents which cause a change to longer reflected wavelengths, and color changes from blue to green, or to brassy-yellow. These changes are thought to be reversible (Fox 1979), but specimens treated with lacto-phenol retain the aberrant colors months after removal from the swelling agent.

*Structure and Sculpture.*— Morphological terms follow Graham (1969) and Richards (1977). Hence, 'postspiracular sclerite' is used for 'prepectus' of authors in the Chalcidoidea. Sculpture types follow Eady (1968), except 'coriarious' is used in preference to 'coriaceous', following the recommendation of Harris (1979, p. 2). Sculpture is best viewed and is here described under diffuse light. Scanning electron micrographs illustrate the major types of sculpture.

The antennae of *Euperilampus* are sexually dimorphic. The funicle is stouter and the scape is expanded distally in males. In some species of *Euperilampus* the anterior face of the male scape is roughened (100-200X magnification), and scanning electron microscopy reveals indentations with pores (Figs. 45-52). Similar sexual characters are found in *Perilampus* and *Steffanolampus*. In males of *Perilampus hyalinus* (Say) (Fig. 64), the anterior surface of the scape is covered with large punctures each of which has a single central pore. In *Perilampus* these structures have been referred to as 'sensorial punctures' (Smulyan 1936). It seems more likely that the pores are glandular openings and not sensory in function; there is no indication of a cuticular peg or dome. Note that many of the punctures are filled with material (Fig. 64). Possibly this substance is the residue of pheromones involved in sexual behavior. Histological studies will be necessary to adequately characterize these structures. I use the term 'punctures' for these structures. In *Euperilampus* there are two to six pores in each puncture (Figs. 46, 48, 52) or punctures are absent (Figs. 42-44). Determination of taxonomic importance of number of pores per puncture must await collection of more material. The distribution of punctures, however, has proved of considerable value in delimiting species.

*Measurements.*— The terms length (L), width (W), and height (H), refer to the maximum value obtained by rotating the specimen. This avoids parallax problems encountered when measuring three-dimensional objects. It is, however, critical to have both endpoints in focus when the measurements are taken. Measurements and their abbreviations used in the text are as follows: EH, eye height, taken in frontal view; MS, length of malar space; A, length of anellus in dorsal view; F1, length of first funicular segment in dorsal view; SL, scape length; SW, scape width; HW, head width, in frontal view; HL, head length, in frontal view, from vertex to lower margin of clypeus; CH, clypeus height; SH, height of supraclypeal area; SW, width of scrobes; OOL, length of ocular-ocellar line; POL, postocellar line, distance between posterior ocelli; PN, length of pronotum along midline; MSC, length of mesoscutum along midline; and SC, length of scutellum along the midline.

## MATERIAL

This study is based on a total of 603 adults of *Euperilampus*, as well as representative material of related taxa. Specimens included are housed in the following collections, which are indicated in the text by the associated acronyms.

AEI: American Entomological Institute, Ann Arbor, MI, U.S.A. 48105 (H.K. Townes)

BMNH: British Museum (Natural History), London, England SW7 5BD (J.S. Noyes)

CAS: California Academy of Sciences, San Francisco, CA, U.S.A. 94118 (P.H. Arnaud, Jr.)

CNC: Canadian National Collection, Ottawa, Canada K1A 0C6 (C. Yoshimoto)

CU: Cornell University, Ithaca, NY, U.S.A. 14853 (L.L. Pechuman)

DCD: D. Christopher Darling, personal collection

FSCA: Florida State Collection of Arthropods, Gainesville, FL, U.S.A. 32611 (L. Stange)

IESM: Instituto Entomologico San Miguel 1663, San Miguel, Argentina (M.A. Fritz)

IML: Instituto Miguel Lillo, Universidad Nacional de Tucuman, Tucuman, Argentina (P. Fidalgo)

KSU: Kansas State University, Manhattan, KS, U.S.A. 66506 (H.D. Blocker)

NHMLAC: Natural History Museum, Los Angeles County, Los Angeles, CA, U.S.A. 90007 (R.R. Snelling)

UA: University of Arkansas, Fayetteville, AK, U.S.A. 72701 (R.G. Chenowith)

UG: University of Guelph, Guelph, Canada N1G 2W1 (D. Pengelly)

UK: Snow Entomological Museum, University of Kansas, Lawrence, KS, U.S.A. 66045 (C.D. Michener)

UNLP: Universidad Nacional de La Plata, 1900 La Plata, Argentina (L. de Santis)

USNM: United States National Museum, Washington, DC, U.S.A. 20560 (E.E. Grissell)

USU: Utah State University, Logan, UT, U.S.A. 84322 (W.J. Hanson)

Other repositories for specimens of *Euperilampus* are as follows: American Museum of Natural History, New York, NY 10024 (M. Favreau); Academy of Natural Sciences of Philadelphia, Philadelphia, PA 19103 (D. Otte); Carnegie Museum of Natural History, Pittsburgh, PA 15213 (G. Ekis); Colorado State University, Fort Collins, CO 80521 (H. E. Evans); Illinois Natural History Survey, Urbana, IL 61803 (W. La Berge); Museum of Comparative Zoology, Harvard University, Cambridge MA 02138 (A. Newton, Jr.); Ohio State University, Columbus, OH 43210 (C. Triplehorn); Pennsylvania State University, University Park, PA 16802 (K. Kim); Southwestern Research Station, Portal, AZ 85632 (V.D. Roth); S.U.N.Y., Syracuse, Syracuse, NY 13210 (M. O'Brien); Texas A & M University, College Station, TX 77843 (S. Merritt); University of Alberta, Edmonton, Canada T6G 2E3 (G.E. Ball); University of Arizona, Tucson, AZ 85721 (F.G. Werner); University of Georgia, Athens, GA 30602 (C. Smith); University of Michigan, Ann Arbor, MI 48109 (T. Moore); and University of Minnesota, St. Paul, MN 55108 (P. Clausen).

I thank all who allowed me to study the material under their care. The curators of the Snow Entomological Museum (UK) and Utah State University Collection (USU) were particularly generous in allowing holotypes described from their material to be deposited in the Smithsonian Collection (USNM). This was requested to allow amalgamation of type material to facilitate further study of the group. The result is that six of the ten extant primary types are at the USNM, with single holotypes in BMNH, CAS, CNC, and IML.

GENUS *EUPERILAMPUS*

*Euperilampus* Walker, 1871: 67. Type Species: *Perilampus gloriosus* Walker, 1862: 375, by monotypy and original designation.

*Euperilampus* (*Euperilampus*): Bouček 1972:90 [as subgenus].

*Euperilampoides* Girault, 1915: 308. Type Species: *Euperilampoides scutellatus* Girault, 1915, by monotypy and original designation [synonymy by Riek, 1966: 1227].

*Euperilampus* (*Euperilampoides*); Bouček 1972:90 [as subgenus].

*Nesoperilampus* Rohwer, 1923: 349. Type species: *Nesoperilampus typicus* Rohwer 1923, by monotypy and original designation [synonymy by Riek, 1966: 1227].

**Diagnosis.**— *Euperilampus* is reliably distinguished from other perilampid genera by having the postspiracular sclerite a narrow triangle (Figs. 35-37), much less than half as wide as the adjacent pronotal collar, and by having the marginal vein distinctly shorter than the postmarginal vein (Figs. 57-59). *Perilampus* (Figs. 60, 61), *Steffanolampus*, *Burksilampus*, and *Monacon* have the postspiracular sclerite at least as wide as the adjacent pronotal collar. All genera except *Euperilampus* have the marginal vein longer than the postmarginal vein (Fig. 62).

The genus *Euperilampus* has been characterized by Riek (1966), Burks (1969) and Bouček (1978). Bouček (1978) has presented a key to world species. Two subgenera were recognized, following Bouček (1972, 1978): *Euperilampus sensu stricto*, bright metallic species with midlobe of mesoscutum and entire scutellum with coarse cross-arcuate rugae, New World; and *Euperilampoides* Girault, dark metallic to black species with thoracic dorsum generally punctate-reticulate, Old World.

Character states of two new species described in this paper (*E. tanyglossa* and *E. aureicornis*) refute this classification. These New World species have the punctate-reticulate sculpture and slightly indicated notauli of the Old World subgenus *Euperilampoides* but are metallic blue-green in color rather than black. Hence, these species are contradictory at the first couplet of Bouček's (1978) key, where the subgenera of *Euperilampus* are separated. As will be discussed, *E. tanyglossa* and *E. aureicornis* are more closely related to *Euperilampus* (*Euperilampoides*) *mediterraneus* than to other New World species. Phylogenetic relationships within the genus, discussed in detail at the end of the paper, are not consistent with recognition of New World and Old World subgenera, *Euperilampus* and *Euperilampoides* (SYNONYMY, REVISED STATUS).

Comparative morphological studies of the Perilampidae have revealed that male genitalia and structure of the labrum (both sexes) characterize *Euperilampus*.

Figures 1 and 2 illustrate major features of the male genitalia. All New World species with the exceptions of *E. gloriosus*, *E. aureicornis*, *E. magnus* (male unknown), and *E. ameca* (male unknown) and the Old World species *E. scutellatus* were examined and allow the following characterization: distinct parameres lacking, basiparamere (Bp) with a patch of strong setae (Ls) distributed on transparent areas (Ld) laterad of ventral lobe (VI). In *Perilampus* (Domenichini 1953), *Steffanolampus* and *Krombeinius* (Darling, unpublished) the parameres are well developed, with the strong setae distributed on these lobes. The presence of distinct parameres is here regarded as the plesiomorphic state for the Chalcidoidea, because this state is widely distributed in many taxa (see Domenichini 1953).

Figure 3 illustrates form of the highly distinctive labrum of *Euperilampus* adults. *Euperilampus triangularis*, *E. krombeini*, *E. scutellatus* (males and females), and *E. tanyglossa* (male) were examined and allow the following characterization: 8-digitate with a deep median incision, each digitus with a strong terminal seta, and with a pair of smaller,



sessile setae located below the level of the digiti. This arrangement differs from that of *Perilampus* (Riek 1966, Domenichini 1969) and *Steffanolampus salicetum* (Darling, unpublished): 10 or 12-digitate, with one digit arising more toward the base of the structure, and the labrum not deeply excised medially, and *Krombeinius eumenidarum* (Darling, unpublished): a single narrow central stalk, with the seven digiti arising apically.

New World species of *Euperilampus* are metallic in color and are distributed from eastern Canada to southern Brazil.

#### KEY TO NEW WORLD *EUPERILAMPUS*

- 1 Entire mesoscutum and scutellum punctate-reticulate (similar in sculpture to the pronotum), notauli indistinctly indicated (Fig. 33); labio-maxillary complex elongate, protruded far beyond the closed mandibles (Fig. 4) ..... 2
- 1' Midlobe of mesoscutum and scutellum with transverse rugae or costae, notauli distinct (Fig. 14); labio-maxillary complex not conspicuously protruded beyond closed mandibles (Fig. 9) ..... 3
- 2 (1) Postspiracular sclerite with three or four weak foveae (Fig. 35); frontal carina weakly divergent and following inner eye margin, inner orbits not markedly narrowed at level of antennal toruli (Fig. 5) [Female funicle dark brown, male funicle yellow] ..... *E. tanyglossa* n. sp., p. 8
- 2' (1) Postspiracular sclerite with a single weak fovea, below fovea with coriarius sculpture; frontal carina oblique, convergent towards inner eye margin, inner orbits markedly narrowed at level of antennal toruli (Fig. 6) [Female and male funicle yellow] ..... *E. aureicornis* n. sp., p. 10
- 3 (1') Apex of scutellum broadly rounded (Fig. 12); lateral wall of scrobes merged smoothly with face (not angulate in lateral view), the inner orbits without well developed longitudinal costae or rugae (Fig. 8) ..... *E. krombeini* Burks, p. 11
- 3' (1') Apex of scutellum acuminate (Figs. 13-16); lateral wall of scrobes merged abruptly with face at level of antennal toruli (angulate in lateral view), inner orbits with well developed longitudinal costae or rugae (Fig. 9) ..... (*E. triangularis* species group) 4
- 4 (3') Scutellum abruptly produced into lanceolate spine, much longer than wide (see Bouček 1978, Fig. 9); metasoma and apex of scutellum bright coppery to golden in color ..... *E. gloriosus* (Walker), p. 15
- 4' (3') Scutellum without abrupt lanceolate spine; entire scutellum and metasoma metallic violet, blues and greens, in some specimens with black areas, not coppery in color ..... 5
- 5 (4') Mesoscutum with distinct contrasting glossy black areas on sidelobe, along notauli, black areas smooth, not roughened (Fig. 14) ..... 6
- 5' (4') Mesoscutum without distinct contrasting black areas on sidelobe along notauli; areas along notauli roughened in many specimens ..... 9
- 6 (5) Fore and mid tibiae yellow, concolorous with tarsi; male antennal scape with distinct punctures on anterior surface, surface roughened (Fig. 45) [Mexican, Female unknown] ..... *E. luteicrus* n. sp., p. 21
- 6' (5) Fore and mid tibiae dark, brown or metallic; male antennal scape with punctures fewer and distinctly separated (Fig. 49,50) ..... 7

- 7 (6') Females [antennal scape not widened apically, Figs. 5-7] ..... *E. brasiliensis* complex
- 7' (6') Males [antennal scape widened apically, Figs. 42,45] ..... 8
- 8 (7') Scape without distinct punctures on anterior surface (Fig. 49), surface smooth; digit of genitalia without large recurved teeth (Fig. 75) ..... *E. brasiliensis* (Ashmead), p. 19
- 8' (7') Scape with distinct punctures on anterior surface (Fig. 50), surface roughened; digit of genitalia with large, recurved teeth (Fig. 74) ..... *E. enigma* n. sp., p. 20
- 9 (5') Axillula with distinct costae, ventral costa merged with posterior margin of axillula (Fig. 53); sculpture on scutellum reduced medially, rugae incomplete (Fig. 16) ..... *E. triangularis* (Say), p. 13
- 9' (5') Axillula smooth or with indistinctly defined costae, not merged with posterior margin of axillula (Fig. 54); sculpture on scutellum not reduced medially, rugae or costae complete (Fig. 13, 15) ..... 10
- 10 (9') Midlobe of mesoscutum with regular cross-arcuate costae (Figs. 13,14) ..... 11
- 10' (9') Midlobe of mesoscutum with irregular rugae (Fig. 15) ..... 12
- 11 (10) Margin of scrobes, sinuous in frontal view, markedly flared at level of antennal toruli (as in Fig. 11); postspiracular sclerite with large centrally located fovea co-extensive with most of upper postspiracular sclerite; sidelobe of mesoscutum with narrow black areas along notauli ..... *E. ameca* n. sp., p. 21
- 11' (10) Margin of scrobes, smoothly curved in frontal view, not markedly flared at level of antennal toruli (Fig. 10); postspiracular sclerite with small fovea located anteriorly, leaving large, smooth triangular area posteriorly (Fig. 31); sidelobe of mesoscutum without black areas along notauli ..... *E. iodes* n. sp., p. 17
- 12 (10') Postspiracular sclerite with distinctly circular fovea, not co-extensive with entire upper postspiracular sclerite (as in Fig. 37), smaller puncture below; scutellum relatively short, SC:MSC = 1.24; margin of scrobes not flared at level of antennal toruli (Fig. 7); large, about 7 mm ..... *E. magnus* n. sp., p. 16
- 12' (10') Postspiracular sclerite with large fovea co-extensive with entire upper postspiracular sclerite (Fig. 32); scutellum longer SC:MSC = 1.34-1.50; margin of scrobes flared at level of antennal toruli (as in Fig. 11); smaller, maximum length 6 mm ..... *E. solox* n. sp., p. 16

## THE NEW WORLD SPECIES OF *EUPERILAMPUS*

### *Euperilampus tanyglossa* n. sp.

(Figs. 4, 5, 18, 25, 28, 33, 34, 35, 41, 42, 56, 58, 69, 70)

*Type Locality*.— México, Jalisco, Zapotlanejo.

*Type Material*.— Holotype (Female, USNM No. 100317): México, Jalisco, Zapotlanejo (Oct. 3 1966, G.E./A.S. Bohart) [Specimen donated to USNM by USU]. Paratypes: Female, four Males, all from México: Morelos, 10 mi E Cuernavaca, (Sept. 15 1972, Hanson/Poff) [Female, USU]; Zacatecas, 5 mi N Tabasco, (Sept. 18 1970; G.E./R.M. Bohart) [2 males: USNM, BMNH]; Jalisco, 15 mi NE Guadalajara, (Sept. 17 1970, G.E./R.M. Bohart) [Male, USU]; Morelos, 6 mi E Cuernavaca, (Sept. 1 1970, Bohart/Hanson) [Male, DCD].

*Diagnosis*.— Combination of an elongate labio-maxillary complex (Fig. 4) and postspiracular sclerite with three or four indistinct foveae (Fig. 35) distinguish this species from

all New World species. *E. aureicornis*, which also has an elongate labio-maxillary complex, has a single, indistinct fovea on the upper postspiracular sclerite and the funicle and clava of the antenna yellow in both sexes (*E. tanyglossa*: female, dark brown; male, bright orange-yellow). *E. tanyglossa* is distinguished from *E. krombeini* and *E. triangularis* group species by the elongate labio-maxillary complex and the punctate-reticulate sculpture of the mesoscutum (Fig. 33; cf. Fig. 12, *E. krombeini* and Fig. 16, *E. triangularis*).

**Geographical distribution.**— This species is distributed in the Central Plateau region of México. The six specimens were collected in five localities and in three different years. All specimens have been collected between 1 September and 3 October. It is likely that this species is widely distributed in the highlands of central México but is rarely collected because adults are present for only about one month of the year. A similar seasonal abundance pattern is found in *E. krombeini*. The host is unknown. The elongate labio-maxillary complex suggests associations with long-corolla flowers.

**Derivation of specific epithet.**— From the Greek (*tany*, 'long' and *glossa*, 'tongue'), a reference to the extremely elongate labio-maxillary complex.

#### *Description.*—

**Female:** Length, 4.8–5.8 mm. Head dark metallic green and violet; antennal scape metallic green, pedicel and anellus brown, funicle and clava dark brown above, underside with light brown areas; labio-maxillary complex dark brown; mandible reddish in middle, dark at base and apex. Mesosoma metallic green and violet; wings strongly darkened throughout; coxae, trochanters and femora dark violet, tibiae dark brown without metallic reflections, tarsi yellow, pretarsi dark brown. Metasoma metallic green.

**Head:** length of malar space 0.25–0.28 eye height; OOL 0.96–1.0 POL; frontal carina narrowly divergent, parallel with inner eye margin, inner orbits not markedly narrowed at level of antennal toruli (Fig. 5); maximum width of scrobes about one-third (0.33–0.35) head width; head transverse, width:height = 1.24–1.28; gena well developed, head widest across genae; vertical costae of inner orbits (parascrobal spaces) short and irregular, surface thus wrinkled, extended onto face and convergent with well developed orbital costae on clypeus as less distinct cross-arcuate costae; clypeus with well developed transverse costae; clypeus transverse, width:height = 1.65–1.74, with sparse short setae except for patch of setae (seven to nine) at each lateral ventral margin, upper margin straight, lower margin emarginate, without tentorial pits; ocular-ocellar region and vertex costate; ocellar triangle almost smooth; supraclypeal area 0.59–0.60 clypeus height, polished with two parallel lines from upper margin of clypeus to antennal toruli; margin of scrobes, in lateral view, merged smoothly with face (Fig. 4); lower tooth of mandible rounded at apex; labio-maxillary complex extremely elongate (Figs. 4, 56). Antennae: pedicel and funicular segments subequal in length; funicular segments transverse, except elongate F1; anellus 0.40 length of F1; scape narrowly linear, length 4.4–5.1 maximum width.

**Mesosoma:** PN:MSC = 0.33–0.36; SC:MSC = 1.13–1.18; dorsum of pronotum and entire mesoscutum punctate-reticulate (Fig. 33), punctures well defined, distinctly circular (Fig. 25) and coalesced in from of transverse rugae only anteriorly on pronotum and along meson of mesoscutum; notauli indistinct; scutellum with short irregular transverse rugae medially, punctate-reticulate laterally; apex of scutellum with distinct and indistinctly septate marginal rim (Fig. 34); sides of scutellum rounded, convergent at an angle of about 70 degrees; underside of scutellum smooth; propodeum vertical, with wide but indistinctly impressed median area, submedian areas coriarius with transverse costae, callus reticulate-rugose (Fig. 18); postspiracular sclerite gradually narrowed ventrally (Fig. 35), not sinuous as in *E. triangularis* group, with three or four indistinct foveae; pronotum with smooth area laterally, below level of foveae on postspiracular sclerite; axilla punctate-reticulate above, below with irregular costae; axillula with well developed longitudinal rugae. Forewing: stigmal vein equal to or slightly longer than marginal vein, postmarginal about 3 times length of marginal vein (Fig. 58).

**Metasoma:** smooth and shining without punctures; setae sparse; T2 with abrupt median concavity and Y-shaped groove (Fig. 28), border between T2 and T3 sinuous and indistinct; T3 more quadrate than in *E. triangularis* group, length about one-half maximum width.

**Male:** Length, 5.2–6.5 mm. Color as in female; except funicle and clava bright orange-yellow and underside of funicle with dark transverse markings. Structure and sculpture as in female except; Head: length of malar space, 0.16–0.22 eye height; head width:height = 1.20–1.24; clypeus width:height = 1.68–1.78; lateral wall of scrobes slightly more developed; antennal scape, in frontal view, expanded only slightly, length 3.5–4.0 maximum width, without distinct punctures (Fig. 42), in lateral view expanded apically with strong setae on outer surface, punctures well developed, surface distinctly roughened (Fig. 41), inner surface with indistinct punctures; pedicel quadrate; funicle stouter. Mesosoma: PN:MSC = 0.34–0.37; SC:MCS = 1.10–1.21. Metasoma: T3 more transverse. Subgenital plate (Fig. 69): elongate, sides gradually divergent, widest along sternite 8, width 1.43–1.50 length along midline [ $n=2$ ]. Genitalia (Fig. 70): digiti with four or five large teeth and single smaller tooth; ventral lobe triangular, apex broadly rounded; lateral demelanized areas of basiparamere large, pigmented median area much longer than length of digiti [ $n=2$ ].

*Euperilampus aureicornis* n. sp.

(Fig. 6)

*Type Locality*.— México, Guerrero, Amula [Almolonga on recent maps].

*Type Material*.— Holotype (Female, BMNH). México, Guerrero, Amula 6000 ft., (Sept., H. H. Smith). Godman-Salvin Coll. 1904.-1. Paratype: Male, same label data as holotype [BMNH].

*Diagnosis*.— Combination of elongate labio-maxillary complex (as in Fig. 4) and postspiracular sclerite with a single fovea distinguish this species from all other New World species. *E. aureicornis* is very similar to *E. tanyglossa* which also has the elongate labio-maxillary complex, but differs in having only a single fovea on the postspiracular sclerite (cf. three or four in *E. tanyglossa*) and funicle and clava of the antennae yellow in the female (cf. brown in *E. tanyglossa*). *E. aureicornis* is distinguished from *E. krombeini* and *E. triangularis* group species by the elongate labio-maxillary complex and the punctate-reticulate sculpture of the mesoscutum (as in Fig. 33; cf. Fig. 12, *E. krombeini* and Fig. 16, *E. triangularis*).

*Geographical distribution*.— This species is known from a single locality at 1829 m. in the Sierra Madre del Sur. The host is unknown.

*Derivation of specific epithet*.— From the Latin (*aureus*, 'golden' and *cornus*, 'horn') referring to the yellow antennae (funicle and clava) in both males and females.

*Description*.—

*Female*: Length, 4.1 mm. Head metallic green, scrobal cavity black; antennal scape metallic green, pedicel dark brown, anellus, funicle and clava golden yellow; labio-maxillary complex dark brown; mandible yellow-brown in middle, dark at base and apex. Mesosoma metallic green with violet reflections on pleurae; wings darkened throughout; coxae with metallic violet reflections, femora, trochanters and tibiae deep brown, tarsi brown. Metasoma dark metallic green, with bronzy reflections.

*Head*: length of malar space 0.23 eye height; OOL equal to POL; frontal carina oblique, convergent toward inner eye margin, inner orbits markedly narrowed at level of antennal toruli (Fig. 6); maximum width of scrobes about one-half (0.46) head width; head transverse, width:height = 1.30; gena well developed, head widest across genae; vertical costae of inner orbits short and irregular, surface wrinkled, extended onto face and convergent with well developed outer orbital costae at clypeus as less developed cross-arcuate costae; clypeus transverse, width:height = 1.54, evenly covered with sparse short setae, smooth and shining with indistinct punctures, transverse costae only at extreme lateral margins, with indistinct tentorial pits at about midpoint of lateral margins of clypeus (Fig. 6); ocular-ocellar region and vertex costate; ocellar triangle almost smooth; supraclypeal area 0.62 clypeus height; margin of scrobes, in lateral view, merged smoothly with face (as in *E. tanyglossa*, Fig. 4); lower tooth of mandible tapered to sharp point; labio-maxillary complex extremely elongate (as in *E. tanyglossa*, Fig. 4); Antennae: pedicel and funicular segments subequal in length; funicular segments transverse except elongate F1; anellus 0.38 length of F1; scape narrowly linear, length 4.8 maximum width.

*Mesosoma*: PN:MSC = 0.36; SC:MSC = 1.11; dorsum of pronotum and entire mesoscutum punctate-reticulate, punctures coalesced in form of transverse rugae only anteriorly on pronotum and along meson of mesoscutum (as in *E. tanyglossa*, Fig. 33); notauli indistinct; scutellum with short irregular transverse rugae medially, punctate-reticulate laterally; apex of scutellum with distinct and weakly septate marginal rim; sides of scutellum rounded, convergent at angle of about 70 degrees; underside of scutellum smooth; propodeum vertical, with shallowly impressed median area, with indistinct transverse costae, raised submedian areas coriarius with transverse costae more dense than in *E. tanyglossa* (cf. Fig. 18), callus reticulate-rugose; postspiracular sclerite gradually narrowed ventrally (as in *E. tanyglossa*, Fig. 35), with single large fovea, and coriarius sculpture below fovea; pronotum with coriarius area laterally, below level of fovea on postspiracular sclerite; axilla punctate-reticulate above, below with irregular rugae; axillula with well developed oblique rugae, similar to *E. triangularis* (cf. Fig. 53). Forewing: stigmal vein slightly longer than marginal, postmarginal about three times length of marginal vein (as in *E. tanyglossa*, Fig. 58).

*Metasoma*: smooth and shining without punctures; setae sparse; T2 with abrupt median concavity, border between T2 and T3 sinuous and indistinct; T3 more transverse than in *E. tanyglossa* length about one-third maximum width.

*Male*: Length, 3.75 mm. Color as in female. Structure and sculpture as in female except; Head: length of malar space, 0.20 eye height; head width:height = 1.35; clypeus width:height = 1.49, tentorial pits much deeper and larger; antennal scape, in frontal view, expanded only slightly, length 4.15 maximum width, without distinct punctures, in lateral view expanded apically with strong setae on lateral surface but without well developed punctures, surface smoother than in *E. tanyglossa* (cf. Fig. 42), inner surface of scape with punctures more distinct and larger than in *E. tanyglossa*; pedicel quadrate. Mesosoma: PN:MSC = 0.36; SC:MSC = 1.11. Genitalia and subgenital plate not examined.

*Euperilampus krombeini* Burks  
(Figs. 8, 12, 17, 29, 36, 38, 43, 59, 68, 73)

*Euperilampus krombeini* Burks, 1969: 79, (Figs. 6,9).

**Type Locality.**— U.S.A., Arizona, Tucson.

**Type Material.**— Holotype (female, USNM No. 69937) [examined]. Paratypes, 3 Females, 6 Males (USNM) [examined; Allotype, USNM No. 69937, misidentified as male; Male paratype deposited in UK].

**Material Examined.**— U.S.A. (39 Females, 28 Males): Arizona (Cochise, Pima Cos.), New Mexico (Hildago Co.). México (6 Females, 2 Males): Sonora, Sinaloa, Chihuahua, Baja California Sur.

**Diagnosis.**— This is the only New World species of *Euperilampus* that lacks well developed longitudinal costae or rugae on the inner orbits (parascrobal spaces) (Fig. 8). This species is distinguished from species of the *E. triangularis* group by the lateral walls of the scrobe, which merge smoothly with the face (Fig. 8; cf. Fig. 9, *E. triangularis*), and from *E. tanyglossa* and *E. aureicornis* by the short labio-maxillary complex and the cross-arcuate sculpture of the midlobe of the mesoscutum (Fig. 12; cf. Fig. 33, *E. tanyglossa*).

**Geographical distribution.**— This species has been collected primarily in the Sonoran and Chihuahuan desert regions. All specimens have been collected in August and September. The host is unknown and many specimens have been collected on flowers.

**Description.**— *E. krombeini* is redescribed primarily to allow comparison with other species, and to include characters not in the original description. Bouček (1978) figured the apex of the scutellum (his Fig. 11). Measurements presented in this redescription are based on 5 paratype males and 5 females (Holotype, 2 paratypes, 2 specimens from the locality of these paratypes, Continental, AZ.) [USNM].

**Female:** Length, 4.2-5.0 mm. Color metallic violet and green, blues rarely seen, generally green with violet reflections, except metasoma which is dark metallic green. Antennal scape metallic blue-green, pedicel, anellus, funicle and clava brown; labio-maxillary complex brown; mandible reddish in middle, dark at base and apex, base with violet reflections; wings darkened throughout; coxae, trochanters, femora and tibiae brown to reddish-brown, usually with distinct metallic reflections, tibiae yellow apically, pretarsi dark brown.

**Head:** length of malar space 0.23-0.27 eye height; OOL 0.64-0.79 POL; maximum width of scrobes 0.34-0.37 head width; head transverse, width:height = 1.23-1.34; gena well developed, head widest across genae; inner and outer orbits (parascrobal spaces) without distinct costae or rugae (Figs. 8,38), costulae only on genae and on face laterad of clypeus; clypeus transverse, width:height = 1.53-1.65, evenly covered with long setae, with indistinct punctures, surface polished, upper margin straight, lower margin emarginate, without tentorial pits; ocular-ocellar region and vertex smooth, with indistinct punctures, and glabrous area laterad of each posterior ocellus; vertex with well developed costae at posterior margin; supraclypeal area 0.46-0.57 clypeus height; lateral wall of scrobes merged smoothly with face (Fig. 8); lower tooth of mandible rounded at apex; base of mandible with distinct punctures; labio-maxillary complex short. Antennae: pedicel and funicular segments subequal in length; funicular segments transverse, except elongate F1; anellus 0.31-0.40 length of F1; scape narrowly linear, length 4.0-4.8 maximum width.

**Mesosoma:** PN:MSC = 0.36-0.37; scutellum short, slightly longer than mesoscutum, SC:MSC = 1.04-1.17; dorsum of pronotum punctate-reticulate, punctures coalesced in form of indistinct irregular transverse costulae medially, lateral punctures distinctly circular; midlobe of mesoscutum with incomplete irregular transverse rugae, reticulate along notauli, sculpture in many specimens less distinct mesad (Fig. 12); sidelobe of mesoscutum completely sculptured, with punctures anteriorly along notauli, laterally reticulate-rugose to rugose posteriorly; notauli distinct; scutellum with well developed cross-arcuate costae, underlying surface with punctures along axillula; apex of scutellum without distinctly septe marginal rim; scutellum broadly rounded (Fig. 12); underside of scutellum smooth; propodeum vertical, with distinct median furrow, submedian areas polished with dense transverse costulae, callus reticulate-rugose (Fig. 17); postspiracular sclerite abruptly narrowed ventrally, sinuous, with shallow fovea coextensive with most of upper postspiracular sclerite, in many specimens with faint punctures below fovea (Fig. 36); axilla reticulate-rugose above, below with irregular rugae; axillula with one to three well developed oblique costae (Fig. 36). Forewing: stigmal vein slightly shorter than marginal, postmarginal about three times length of marginal vein (Fig. 59).

**Metasoma:** T2 with median longitudinal row of closely spaced punctures extended two-thirds distance to T2/T3 border and with lateral arcuate lines of punctures joined to apex of median row (Fig. 29); T2 with sparse setae, without punctures, border between T2 and T3 sinuous and indistinct; T3 more quadrate than in *E. triangularis* group, length about one-half maximum width (0.52-0.57), with lateral patches of setae, and distinct punctures; T4 and T5 with well developed punctures extended transversely across anterior surface of terga.

*Male:* Length, 3.7-4.6 mm. Color as in female. Structure and sculpture as in female, except; Head: antennal scape, in frontal view, expanded only slightly, length 3.9-4.4 maximum width, without punctures, outer surface with strong setae and roughened with punctures (Fig. 43), inner surface without distinct punctures; pedicel quadrate; anellus relatively shorter, 0.10-0.26 length of F1; funicle stouter. Mesosoma: PN:MSC = 0.33-0.40; SC:MSC = 1.08-1.26. Metasoma: T3 more transverse, length about one-third width. Subgenital plate (Fig. 68): transverse, sides gradually divergent, widest along sternite 8, width 2.05-2.23 length along midline [ $n=4$ ]. Genitalia (Fig. 73): digiti with three or four large teeth and single smaller tooth; ventral lobe acuminate, apex broadly rounded; lateral demelanized areas of basiparamere large, pigmented median area about equal in length to digiti.

### *Euperilampus triangularis* group

*Diagnosis.*— This species group is characterized by massive scrobal walls which are sharply angulate at the level of the antennal toruli and merge abruptly with the face (Fig. 9). The apex of the scutellum is acuminate (Figs. 13-16), not broadly rounded as in *E. krombeini* (Fig. 12). The labio-maxillary complex is short (Fig. 9), not elongate as in *E. tanyglossa* and *E. aureicornis* (Fig. 4).

*Geographical distribution.*— This species group is widely distributed in eastern North America, into central Québec, and south to Florida; in the montane regions of México and in the montane regions of southern Brazil, northern Argentina, eastern Bolivia and Paraguay. There are no specimens from northern South America or Central America. This disjunction may simply be due to a paucity of montane collections.

*Description.*— A group description is provided, based on the presently included species: *E. triangularis*, *E. gloriosus*, *E. brasiliensis*, *E. enigma*, *E. luteicrus*, *E. ameca*, *E. iodes*, *E. solox*, and *E. magnus*. Measurements and ratios are presented in general terms and the ranges of numerical values are listed in Table 1 for the species represented by multiple specimens. The group descriptors are not repeated in the descriptions of the included species; a full description of each species is the group description with the appropriate numerical values from Table 1 and the species description.

*Female:* Length, 3.0-7.5 mm. Head, mesosoma and metasoma metallic (iridescent) violets, blues and greens with violet reflections, in some species with contrasting glossy black areas on head and mesosoma; antennal scape metallic green, pedicel brown with metallic reflections, anellus, funicle and clava dark brown, labio-maxillary complex dark brown; mandible, basally metallic, distally reddish-brown; wings darkened throughout; coxae, trochanters, femora and tibiae dark with metallic reflections (fore and mid tibiae yellow in *E. luteicrus*); distal end of tibiae light brown, tarsi yellow, pretarsi dark brown.

*Head:* Length of malar space about one-third eye height; lower margin of eyes extended to top of clypeus; base of mandible with distinct punctures; OOL approximately equal to POL; maximum width of scrobes one-third to one-half head width; head transverse, width:height = 1.0-1.2; vertical costae of inner orbits (parascrobal spaces) well developed, extended onto face and convergent with outer orbital costae on clypeus (Fig. 9); clypeus transverse, width about 1.5 times height, with costae at lateral margins, evenly covered with long setae; upper margin concave or straight, lower margin emarginate, without tentorial pits; vertex with well developed carina(e) at posterior margin and glabrous area laterad of each posterior ocellus; supraclypeal area about one-half clypeus height, glabrous and polished; lateral wall of scrobes merged abruptly with face, at level of antennal toruli (Fig. 9); lower tooth of mandible tapered to sharp point; labio-maxillary complex short (Figs. 9,55), extended just beyond mandibles. Antennae: pedicel and funicular segments subequal in length; funicular segments transverse except elongate F1; relative length of anellus to F1 diagnostic; scape narrowly linear, length about 5-6 times maximum width.

*Mesosoma:* sculpture diagnostic; pronotum one-third to one-half length of mesoscutum; scutellum longer than mesoscutum, SC:MSC diagnostic; notauli distinct; apex of scutellum with marginal rim; propodeum vertical, with median impressed foveae and raised submedian areas with transverse costae, callus reticulate-rugose (Fig. 19); postspiracular sclerite abruptly narrowed ventrally, sinuous, with single large fovea dorsally, size and shape of which is diagnostic, with some smaller punctures below fovea in some species. Forewing: stigmal vein shorter than marginal, postmarginal vein about three times length of marginal vein (Fig. 57).

*Metasoma:* smooth and shining, T2, T4, and T5 evenly covered with setae, T3 with lateral patches of setae, T4 with indistinct punctures at base of setae, punctures on T5 indistinct or well developed; T2 smoothly concave (Fig. 27), border between T2 and T3 sinuous and indistinct; T3 transverse, length about one-third maximum width (0.33-0.39).

*Male*: Length, 2.0-5.0 mm. Color as in female. Structure and sculpture as in female except; Head: relative length of malar space to eye height smaller, antennal scape, in frontal view, expanded slightly apically, length about four times maximum width; distribution of punctures and setae diagnostic; pedicel quadrate, shorter than F1; relative length of anellus to F1 shorter; funicle stouter. Mesosoma: costae on submedial areas of propodeum more prominent. Metasoma: T3 more transverse. Subgenital plate: subquadrate, abruptly expanded along sternite 8 (Fig. 67), width:length, 1.30-1.83 (n=15). Genitalia: diagnostic.

*Euperilampus triangularis* (Say)

(Figs. 1, 2, 3, 9, 11, 16, 19, 20, 21, 27, 37, 39, 44, 53, 55, 57, 67)

*Perilampus triangularis* Say, 1828:78. [Type lost].

*Euperilampus triangularis*; Crawford, 1914:69.

*Type Locality*.— U.S.A., Indiana.

*Material Examined*.— U.S.A. (310 Females, 182 Males): Alabama, Arkansas, Connecticut, District of Columbia, Florida, Illinois, Indiana, Iowa, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, South Dakota, Texas, Vermont, Virginia, West Virginia, Wisconsin. Canada (8 Females, 6 Males): Québec: Aylmer, Lac Chicobi, Montreal. Ontario: Ottawa, Point Pelee, Ruby.

*Notes about synonymy*.— Burks (1969) compared *E. triangularis* with *E. krombeini* and illustrated the head of *E. triangularis* (his Fig. 11) as *E. hyalinus*. (*lapsus calami*) in the figure legends. Bouček (1978) illustrated the apex of the scutellum of *E. triangularis* (his Fig. 10). *E. triangularis sensu* Bouček is coextensive with my *E. triangularis* species group.

*Diagnosis*.— This species is reliably distinguished from other members of the *E. triangularis* group by having a concolorous mesoscutum, i.e., without contrasting black areas on the sidelobe, and axillulae with distinct costae, the most ventral of these merging with the posterior border of the axillulae (Fig. 53; cf. Fig. 54, *E. brasiliensis*). Sculpture on the scutellum is less developed along the midline, the rugae incomplete (Fig. 16; cf. Fig. 13, *E. iodes* and Fig. 14, *E. brasiliensis* and Fig. 15, *E. solox*).

*Geographical distribution*.— This species is widely distributed in eastern North America, extending to western South Dakota (Custer Co., Lawrence Co.), eastern Kansas (Riley Co.), and east Texas (Galveston Co.). The distribution matches closely the extent of broadleaf deciduous forests. Western extremes in the range are along tributaries of the Missouri River: riparian areas with broadleaf deciduous forests. Representative collection dates are as follows: New York, June 30 - September 1; Massachusetts, June 24 - September 10; Québec, July 1 - August; Kansas, June 20 - July 1.

*E. triangularis* has been collected frequently in Highlands Co., Florida at the Archbold Research Station [FSCA]. This is an area of needleleaf evergreen forest and violates the distributional correlates established above. These specimens show some morphological peculiarities (see 'Variation' section). Collection dates also differ dramatically from the northeastern material and range from March 2 - May 30 (based on 70 specimens). Other specimens from Florida (all northern Florida) also were collected between these dates. This species has not been recorded from Georgia, South Carolina, Mississippi, Tennessee, Kentucky or Louisiana. Excluding Florida, North Carolina is the most southern record of this species along the east coast, and specimens have been taken May 16 (Columbus Co., coastal), May 20 (Black Mts.), July 27 (Haywood Co., Blue Ridge Mts.), September 23 (Buncombe Co., Blue Ridge Mts.).

The temporal separation of *E. triangularis* into spring and late summer collection dates is probably related to overwintering of hosts in northern and montane areas. Direct development of the hosts in the southern extremes of the range would explain occurrence of specimens in April and May. Unfortunately the host(s) of *Euperilampus triangularis* in Florida is unknown.

Bouček examined North American material and specimens from Santa Catarina, Brazil (Nova Teutonia). Bouček (1978) lists material from Colorado, as does Peck (1951, 1963), and Burks (1979), apparently in reference to Ashmead (1890). I have seen no specimens from the Rocky Mountains or from Colorado.

*Host associations.*— *Euperilampus triangularis* is a secondary parasite (hyperparasite) of the fall webworm, *Hyphantria cunea* (Drury) [Arctiidae]. Warren and Tadic (1970) reared *E. triangularis* as a parasitoid of *Hyposoter fugitivus* (Say) [Ichneumonidae] which attack the fall webworm as primary parasitoids (13 females, 28 males). This material was misidentified as *Perilampus hyalinus*, although *P. hyalinus* was also reared from *Hyposoter* (six females, two males) and other primary parasitoids [series examined, UA]. Rearings of *Hyphantria cunea* in New York (Darling, unpublished) have also yielded both *P. hyalinus* and *E. triangularis*. Other parasitoids obtained in the New York rearings included only Tachinidae [*Eusisyropa blanda* (O.S.), *Blondelia hyphanthiae* (Tothill) and *Mericia ampelus* (Wlk.)] and Ichneumonidae [*Therion* spp. and *Sinophorus validus* (Cresson) complex] [CU, UG, DCD]. The host of *Euperilampus triangularis* in New York has yet to be determined. I also have seen a specimen of *E. triangularis* reared from *H. cunea* from Ruby, Ontario, Canada [CNC].

*Description.*— The redescription and measurements are based on 17 females and 18 males, three specimens of each sex from the following six localities, except where noted otherwise: Florida, Highlands Co., Archbold Biological Station [FSCA]; Virginia, Arlington Co., Kearney Sta. [USNM]; Arkansas, Washington Co., Fayetteville, Ex: *Hyposoter* spp, parasite of *Hyphantria cunea* [UA]; Canada, Québec, various localities, and 1 Female from Ruby, Ont. [CNC, USNM]; Kansas, various localities (only 2 Females examined) [UK, KSU, USNM]; New York, Seneca Co., Geneva, Ex: culture of *Hyphantria cunea* [DCD, UG].

*Female:* Length, 2.9-6.3 mm. Color ranging from blue-violet to blue-green, with violet reflections on mesoscutum and green reflections on metasoma, without contrasting black areas on sidelobe of mesoscutum.

*Head:* maximum width of scrobes 0.28-0.35 head width; margin of scrobes, in frontal view, sinuous and flared at level of antennal toruli (Fig. 11); inner orbital costulae irregularly spaced, wavy to rugose (Fig. 9), convergent toward posterior ocellus and not extended through ocular-ocellar region (Fig. 21); outer orbital costae various, restricted to malar region or extended to vertex, less developed above; vertex almost completely sculptured (punctures and indistinct rugae), except for glabrous area laterad of each posterior ocellus; clypeus with indistinct arcuate costae at extreme lateral margins, punctures well developed and dense, surface appearing roughened. Antennae: anellus 0.18-0.25 length of F1, relatively shorter than in other species (see Table 1).

*Mesosoma:* scutellum longer than mesonotum, SC:MSC = 1.42-1.60; dorsum of pronotum punctate-reticulate, punctures coalesced in form of transverse rugae anteriorly (as in Fig. 26), punctures along midline polygonal, not distinctly circular; midlobe of mesoscutum with transverse rugae, more irregular (reticulated) posteriorly, sidelobe of mesoscutum posteriorly rugose, anteriorly along notauli roughened with irregular punctures, laterally punctate-reticulate; scutellum with arcuate rugae, less developed along midline, and longitudinally rugose-reticulate laterally (Fig. 16); apex of scutellum with distinctly septe marginal rim; scutellum acuminate, sides convergent at about 60 degrees; underside of scutellum sculptured (Fig. 39); median area of propodeum with deeply impressed foveae, in form of distinct X-shape (Fig. 19), submedian areas polished with cross-arcuate costulae throughout; postspiracular sclerite with large, round, centrally-located fovea (Fig. 37); axilla reticulate-rugose above, rugose below; axillula smooth and shining, with one to three short oblique costae, ventral costa in most specimens merged with posterior border of axillula (Fig. 53).

*Metasoma:* T5 with indistinct punctures.

*Male:* Length, 2.3-5.2 mm. Color as in female. Structure and sculpture as in female except, Head: antennal scape, in frontal view, expanded slightly apically, smooth (Fig. 44); anellus relatively smaller, 0.10-0.15 length of F1, relatively shorter than other species (see Table 1). Mesosoma: propodeum more coarsely sculptured with more prominent cross-arcuate costae. Genitalia (Figs. 1,2): digiti with three, four, or five large teeth and two or three smaller teeth; ventral lobe rounded, not distinctly acuminate but in few specimens notched at apex; lateral demelanized areas of basiparamere large and quadrate, not reduced laterally, pigmented median area shorter than length of digiti [n-17].

*Variation.*— The reared series of *E. triangularis* from Arkansas differs considerably from wild caught specimens. The Arkansas series consists of extremely small individuals about 3 mm in length. In these specimens the sculpture of the propodeum is quite distinctive with the median triangle about half the height of the propodeum (compare Fig. 20, reared from



*Hyposoter* and Fig. 19, wild caught specimens from Archbold Research Station). Of the total material examined, only five wild caught specimens (1.1%) are as small as this reared material ( $MSC < .75$  mm). In these wild caught specimens, the propodeum is of the standard configuration, with the median triangle quite small. It is possible that the rearing conditions were sub-optimal, resulting in these abnormally small individuals, with the associated variation in propodeum structure. All wild caught specimens from Arkansas ( $n=3$ ) are of normal size (5.00-5.83 mm) and the propodeal triangle is not enlarged. A single small specimen from Ruby, Ontario [CNC], again reared from *H. cunea*, has the unusually large propodeal triangle.

Florida specimens also differ from northeastern material. Inner orbital costae and transverse rugae of the midlobe of the mesoscutum are very irregular, especially in males. Florida specimens also have relatively longer scutella, SC:MSC, than specimens from other areas (males, 1.69-1.75; all other localities, 1.42-1.60. females, 1.55-1.56; all other localities, 1.42-1.55). Male genitalia of New York specimens ( $n=6$ ), Florida ( $n=6$ ), Virginia ( $n=2$ ), and Arkansas, reared from *Hyposoter* ( $n=2$ ), show no consistent differences.

The apex of the scutellum is quite aberrant in four specimens. Variants include deeply cleft and bilobed apices, and asymmetrical developments of the normal acuminate apex. The most striking variant is a deeply bilobed apex which is bent under the vaulted part of the scutellum so that the marginal rim is not visible in dorsal view. This specimen, a female from Highlands Co., Florida, was among four normal specimens from the same Malaise trap collection [FSCA]. In addition, the reared series from Arkansas have many specimens with truncate scutella, shallowly cleft at the apex.

The status of the Florida population will have to be reconsidered when the host association(s) is determined. Possibly this population represents a sibling species related to *E. triangularis*. Description of such a sibling species from eastern North America will present 'exceptional circumstances', as outlined by Article 75 of the International Code of Zoological Nomenclature. A neotype will have to be designated for Say's species, to fix the name with the northern population. A suitable topotypic specimen is in the Cornell collection, [Female: Indiana, Madison, July 29 1957, H.E. Evans]. This specimen agrees with all the particulars of this redescription.

### *Euperilampus gloriosus* (Walker)

*Perilampus gloriosus* Walker, 1862:375.

*Euperilampus gloriosus*; Walker, 1871:67.

*Euperilampus gloriosus*; Bouček, 1978:304 [lectotype designation].

*Type Locality*.— México.

*Type Material*.— Lectotype (male, BMNH) [not examined].

*Diagnosis*.— The following is based on notes of A.B. Gahan [USNM], Burks (1969), and Bouček (1978). This species can readily be distinguished from all other New World species of *Euperilampus* by the scutellum, which is rather abruptly produced into a lanceolate spine (Fig. 9 in Bouček 1978) and by the bright coppery to fiery golden color of the apex of the scutellum and the metasoma.

The species is known only from the type material. The specimen was collected by M. Sallé; the exact locality in México is apparently unknown.

*Euperilampus magnus* n. sp.

(Fig. 7)

*Type Locality*.— México, Chiapas, Chiapa de Corzo.

*Type Material*.— Holotype (Female, CAS): Mexico, Chiapas, Municipio Chiapa de Corzo, El Chorreadero, 670 m (Aug 16 1976, DE/JA Breedlove).

*Diagnosis*.— The relatively short scutellum,  $SC:MSC = 1.24$ , separates the holotype from all species except the *E. brasiliensis* complex. The specimen differs from *E. brasiliensis* complex females by the absence of contrasting black areas on the sidelobe of the mesoscutum and by the margin of the scrobes not being flared at the level of the antennal toruli (Fig. 7). The reliability of size in recognizing this species must await further collecting. This specimen is 1.2 times larger than any other New World specimen.

*Geographical distribution*.— The type locality is in the interior highlands of Chiapas and is the only Mexican locality for *Euperilampus*, east of the Isthmus of Tehuantepec.

*Derivation of specific epithet*.— From the Latin, with reference to the large size of the holotype.

*Description*.—

*Female*: Length, 7.5 mm. Color ranging from blue-violet to blue-green, with violet and green reflections, and glossy black posteriorly on vertex, but without contrasting black areas on sidelobe of mesoscutum.

*Head*: Length of malar space 0.36 eye height;  $OOL = 0.83 POL$ ; maximum width of scrobes 0.35 head width; margin of scrobes, in frontal view, smoothly curved, not flared at level of antennal toruli (Fig. 7); gena very well developed, head widest across genae; head transverse, width:height = 1.2; inner orbital costulae irregularly spaced, convergent on posterior ocellus and not extended through ocular-ocellar region (as in *E. triangularis*, Fig. 21); outer orbital costulae extended past point of maximum width of eye but not to vertex; vertex almost smooth, posteriorly with seven transverse costulae; clypeus transverse, width:height = 1.55, with indistinct arcuate costae at extreme lateral margins, punctures distinct and dense, surface appearing roughened; supraclypeal area 0.47 clypeus height. Antennae: anellus 0.18 length of F1; scape narrowly linear, length 4.6 times maximum width.

*Mesosoma*:  $PN:MSC = 0.50$ ; scutellum slightly longer than mesoscutum,  $SC:MSC = 1.24$ ; dorsum of pronotum punctate-reticulate, interspaces widened and punctures distinctly circular; midlobe of mesoscutum rugose, transverse rugae less wavy than in *E. solox* (cf. Fig. 15), sidelobe of mesoscutum posteriorly rugose, anteriorly along notauli roughened with irregular punctures, laterally punctate-reticulate; scutellum with arcuate rugae, less distinct on disk; apex of scutellum with distinctly septate marginal rim; scutellum acuminate, sides convergent at about 70 degrees; underside of scutellum smooth; median area of propodeum shallowly impressed, without deep foveae, submedian areas with swirling costae; postspiracular sclerite with large, round, centrally-located fovea, and smaller puncture below; axilla reticulate-rugose above, rugose below; axillula smooth and shining, with one to three short oblique costae not merged with posterior border.

*Metasoma*: T5 with distinct punctures.

*Male*: UNKNOWN.

*Euperilampus solox* n. sp.

(Figs. 15, 32, 47, 48, 76)

*Type Locality*.— Argentina, Tucuman, Tacanas.

*Type Material*.— Holotype (Female, IML): Argentina, Tucuman, Tacanas (Nov. 5 - 30 1968, L. Stange). Paratypes: (4 Females, 2 Males) all from Argentina. Tucuman, Trancas to Tacanas (Nov. 1-30, Stange) [Female, BMNH], (Jan., Arnau) [Female, USNM]. Salta: Alemania (April, Stange/ Porter) [Female, CNC, identified as *Euperilampus triangularis* (Say) in Fidalgo 1980: 194]. Tucuman: San Pedro Colalao (Foerster), [Female, IESM]. Salta: Cerro San Bernardo (Feb., Monrós/ Willink). [Male, IML]. Tucuman: Trancas, San Pedro Colalao (Feb., Arnau) [Male, CNC].

*Diagnosis*.— *E. solox* is recognized by the reticulate-rugose sculpture of the midlobe of the mesoscutum (Fig. 15). The mesoscutum does not have contrasting black areas, which distinguishes the species from the *E. brasiliensis* complex. The fovea of the postspiracular sclerite is large but indistinctly impressed (Fig. 32) and the margins of the scrobes are flared at

the level of the antennal toruli (as in Fig. 11), distinguishing this species from *E. iodes* (cf. Fig. 10. *E. iodes*). *E. solox* does not have the reduced sculpture on the disk of the scutellum, which is characteristic of *E. triangularis* (Fig. 15; cf. Fig. 16. *E. triangularis*).

**Geographical distribution.**— *E. solox* is known only from northern Argentina. The host is unknown.

**Derivation of specific epithet.**— From the Latin, *solox*, for ‘coarse or rough’ with reference to the irregular sculpture of the mesoscutum.

**Description.**—

**Female:** Length, 5.4–6.2 mm. Color predominantly blue-green, with violet reflections, contrasting black areas restricted to vertex, not on mesoscutum.

**Head:** maximum width of scrobes 0.41–0.43 head width; margin of scrobes, in frontal view, sinuous and flared toward eye margin at level of antennal toruli (as in *E. triangularis*, Fig. 11); inner orbital costae rugose, extended to ocular-ocellar region; outer orbital costulae extended to vertex, less distinct above; vertex completely sculptured (coarse punctures and indistinct rugae), except for glabrous area laterad of each posterior ocellus; clypeus with indistinct arcuate costae at extreme lateral margins, punctures distinct and dense, surface appearing roughened. Antennae: anellus 0.26–0.35 length of F1.

**Mesosoma:** scutellum longer than mesoscutum, SC:MSC = 1.38–1.48; dorsum of pronotum punctate-reticulate, punctures not coalesced in form of distinct transverse rugae anteriorly, punctures circular or polygonal, interspaces widened; mesoscutum reticulate-rugose, with very irregular rugae anteriorly on midlobe (Fig. 15) and posteriorly on sidelobe, sculpture reduced along notauli; scutellum with irregular cross-arcuate rugae, laterally reticulate-rugose; apex of scutellum with distinctly septate marginal rim; scutellum acuminate, sides convergent at about 70 degrees; underside of scutellum sculptured at apex; median area of propodeum with deeply impressed foveae, in form of distinct V-shape, submedian areas polished, with seven or eight well developed and evenly distributed cross-arcuate costae; postspiracular sclerite with shallow circular fovea co-extensive with most of upper postspiracular sclerite (Fig. 32); axilla reticulate-rugose above, rugose below; axillula smooth and shining, without costae extended to posterior border (as in *E. brasiliensis*, Fig. 54).

**Metasoma:** T5 with well developed punctures, stronger than in other species of *E. triangularis* group.

**Male:** Length, 3.7–4.2 mm. Color as in female. Structure and sculpture as in female except, **Head:** Antennae: anellus relatively smaller; scape, in frontal view, expanded apically, with distinct punctures on anterior and inner surfaces, outer surface with strong setae, surface roughened (Figs. 47, 48). Genitalia (Fig. 76): digiti with two to five large teeth and two smaller teeth; ventral lobe broadly rounded, notched in single specimen; lateral demelanized areas of basiparamere large and quadrate, not reduced laterally, pigmented median area slightly shorter than digiti [ $n=2$ ].

**Variation.**— The sculpture of the mesonotum is less distinct in some specimens. The female specimen (USNM: Trancas to Tacanas) is a deep emerald green color due to cleaning the specimen in lacto-phenol to remove a fungal coating.

*Euperilampus iodes* n. sp.

(Figs. 10, 13, 23, 24, 31, 51, 52, 72)

**Type Locality.**— Brazil, Santa Catarina, Nova Teutonia.

**Type Material.**— Holotype (Female, CNC No. 17004): Brazil, Santa Catarina, Nova Teutonia, 300 - 500 m, (Feb. 1968, F. Plaumann). Paratypes (4 Females, 2 Males), same locality and collector as holotype (Aug., Sept., Oct.) [BMNH, CNC, IML].

**-Additional Material Examined.**— Brazil, São Paulo, Barreiro, Serra de Bocaina, 1650 m (Sept., Alvarenga and Seabra) [Female, AEI]. México, Jalisco, 15 mi. S. Lagos de Moreno (Aug., 1962) [Female, NHMLAC].

**Diagnosis.**— This is the only species with the fovea of the postspiracular sclerite small and located on the anterior portion of the sclerite, leaving a large smooth triangular area posteriorly (Fig. 31). The concolorous mesoscutum and the relatively longer scutellum distinguish *E. iodes* from the *E. brasiliensis* group (see Table 1). This species differs from *E. solox* in having the margin of the scrobe smoothly curved, not flared at the level of the antennal toruli (Fig. 10; cf. Fig. 11, flared at level of toruli), and more regular sculpture on the mesoscutum (Fig. 13; cf. Fig. 15, *E. solox*). This species has the sculpture of the scutellum complete (Fig. 13), not reduced on the disk of the scutellum as in *E. triangularis*, (Fig. 16). *E. iodes* is the only species

with costae extending through the ocular-ocellar region along the eye margin (Figs. 23, 24; cf. Fig. 21, *E. triangularis* and Fig. 22, *E. brasiliensis*).

**Geographical distribution.**— *E. iodes* is sympatric with *E. brasiliensis* at Nova Teutonia, Brazil. Specimens are known only from México and Brazil, and the host is unknown. The description and measurements are based on the type material.

**Derivation of specific epithet.**— From the Greek, *iodes*, 'violetlike', with reference to color of adults of this species.

**Description.**—

**Female:** Length, 4.2-5.4 mm. Color predominantly blue-violet, with green reflections on scrobal cavity, supraclypeal area, pleuron of mesosoma and metasoma; without contrasting black areas on vertex and mesoscutum.

**Head:** maximum width of scrobes 0.38-0.40 head width; margin of scrobes, in frontal view, smoothly curved, not flared at level of antennal toruli (Fig. 10); inner orbital costae regularly spaced, outermost costulae extended around top of eye, through ocular-ocellar region (Figs. 23, 24); outer orbital costulae extended to vertex, less distinct above, but much more distinct along eye margin; vertex almost smooth, posteriorly with transverse costae; clypeus with well developed costae at lateral margins, punctures indistinct and sparse, surface smooth. Antennae: anellus 0.27-0.32 length of F1.

**Mesosoma:** scutellum longer than mesoscutum, SC:MSC = 1.38-1.50; dorsum of pronotum punctate-reticulate, punctures coalesced in form of distinct transverse rugae anteriorly, punctures along midline polygonal, not distinctly circular; midlobe of mesoscutum and entire scutellum with incomplete but regular cross-arcuate costae, sidelobe of mesoscutum posteriorly roughened, anteriorly along notauli with indistinct irregular punctures, laterally punctate-reticulate to rugose posteriorly (Fig. 13); apex of scutellum with distinctly septate marginal rim; scutellum acuminate, sides convergent at about 70 degrees; underside of scutellum sculptured at apex; median area of propodeum with deeply impressed foveae, in form of distinct V-shape, submedian areas smooth and shining, with indistinct cross-arcuate costulae dorsally; postspiracular sclerite with small fovea extended about one-half upper postspiracular sclerite, fovea anterior on postspiracular sclerite, with smooth triangular area in upper posterior corner (Fig. 31), axilla rugose; axillula smooth and shining, many specimens with 1-3 short costae.

**Metasoma:** T5 with indistinct punctures.

**Male:** Length, 3.7-3.9 mm. Color as in female, but contrasting black areas on vertex. Structure and sculpture as in female except, Head: Antennae: anellus relatively smaller, 0.14-0.25 length of F1; scape, in frontal view, expanded slightly apically, punctures on anterior and inner surfaces, outer surface with strong setae, surface roughened (Figs. 51, 52). Mesosoma: sculpture of sidelobe of mesoscutum either female condition or completely rugose along notauli; propodeum more coarsely sculptured with more prominent cross-arcuate costae and with fovea on submedian areas. Genitalia (Fig. 72): digiti with five large teeth and two smaller teeth; ventral lobe acuminate, not broadly rounded; lateral demelanized areas of basiparamere large and quadrate, pigmented median area shorter in length than digiti [ $n=2$ ].

**Variation.**— The specimen from Barreiro, Brazil, differs from the type series in having the fovea of the postspiracular sclerite somewhat larger, and the inner orbital costae less developed along the top of the eye. The Mexican specimen is similar to the Barreiro specimen, but the lateral wall of the scrobe is not as prominent in lateral view and the wings are hyaline, not distinctly darkened.

### *Euperilampus brasiliensis* complex

**Diagnosis.**— All species have black areas on the sidelobe which contrast with the otherwise metallic color. These areas are quite large and occupy the anterior one-half of the sidelobe, except in *E. ameca* (reduced to a narrow band along the notauli). Scutella are relatively shorter than in all other species of the *E. triangularis* group (Fig. 14), SC:MSC ranging from 1.19 to 1.31. The only exception is the holotype of *E. luteicrus*, SC:MSC = 1.45. The short scutella result in the sides of the scutellum being convergent at an angle of about 75 degrees (60 - 70 degrees in other species of the *E. triangularis* group). The upper postspiracular sclerite has a single large fovea which is not distinctly circular (Fig. 30).

**Taxonomic note.**— This complex is defined to encompass species related to *E. brasiliensis* as diagnosed above (*E. enigma*, *E. luteicrus*, and *E. ameca*). The paucity of material has presented many problems; all species are allopatric, and the three new species are based on single specimens. Association of sexes is further complicated by the fact that the type material

of *E. brasiliensis* is represented only by females.

Females of this complex from central South America are indistinguishable, but two distinct forms of males are present. A series of seven females from Nova Teutonia, Santa Catarina, Brazil, are here regarded as conspecific with the type of *E. brasiliensis* [type locality--Chapada, Brazil]. Three males from Nova Teutonia appear to be conspecific and are here described as the male of *E. brasiliensis*. A very distinctive male from Roboré, Bolivia, is described as *E. enigma* n. sp. This could be the male of *E. brasiliensis*; if so, the Nova Teutonia material would represent a new species. I decided to treat the Bolivian male as a new species, since this is a more conservative solution. The other possibility would be to associate the Bolivian male with the type material of *E. brasiliensis*, and to describe a new species for the Nova Teutonia material based on differences from the associated, Bolivian male. As treated here, *E. brasiliensis* and *E. enigma* are separated by the Paraguay River.

This complex is represented in México by two new species, each based on a single specimen. The hosts are not known for any species of this complex.

*Euperilampus brasiliensis* (Ashmead) n. comb.

(Figs. 14, 22, 26, 30, 40, 49, 54, 75)

*Perilampus brasiliensis* Ashmead, 1904: 467 (Plate 34, Fig. 4).

**Type Locality.**— Brazil, Chapada [Matto Grosso]. [Holland (1919:482) discusses the various expeditions of H.H. Smith. The 1881-1886 trip to Brazil spent considerable time along the upper waters of the Rio Paraguay and Rio Guapore in western Brazil near Chapada and Matto Grosso. Much of this material went to the Carnegie Museum and was studied by Ashmead.]

**Type Material.**— Lectotype (Female, USNM No. 56960) [Present designation]: Chapada, April, H.H. Smith Coll. Paralectotype (Female, USNM Paratype No. 56960): Chapada, Nov.

**Material Examined.**— Brazil (12 Females, 4 Males); Santa Catarina, Nova Teutonia 300 - 500 m. (Jan. - June, August, September; F. Plaumann) [AEI, BMNH, CNC, UK]. Argentina (1 Female, 1 Male) Misiones: Loreto (Dec.) [Female, UNLP], Iguazu (March) [Male, IML; identified as *Euperilampus triangularis* (Say) in Fidalgo 1980: 194]. Paraguay (1 Female): Independencia (Sept.) [UNLP].

**Diagnosis.**— Only the male of this species can be distinguished from other members of the *E. brasiliensis* complex. The male genitalia lack enlarged, recurved teeth on the digitus (Fig. 75; cf. Fig. 74, *E. enigma*), and the scape of the antenna has very weak punctures on the inner surface (Fig. 49; cf. Fig. 50, *E. enigma*; Figs. 45, 46, *E. luteicrus*).

**Description.**— The redescription and measurements are based on the type material and the specimens from Nova Teutonia.

**Female:** Length, 4.6-6.3 mm. Color predominantly blue-green, with violet reflections. Vertex, midlobe and sidelobe of mesoscutum, with contrasting glossy black areas.

**Head:** maximum width of scrobes 0.37-0.44 head width; margin of scrobes, in frontal view, sinuous and flared at level of antennal toruli (as in *E. triangularis*, Fig. 11); head widest across eyes; inner orbital costae not convergent on posterior ocellus or extended around top of eye, ended abruptly at ocular-ocellar region (Fig. 22); outer orbital costae short, largely confined to malar region; vertex almost smooth, posteriorly with transverse costae; clypeus with indistinct arcuate costae at extreme lateral margins, punctures indistinct, surface appearing smooth and polished. Antennae: anellus 0.23-0.33 length of F1.

**Mesosoma:** scutellum slightly longer than mesoscutum, SC:MSC = 1.19-1.31; dorsum of pronotum punctate-reticulate, punctures coalesced in form of transverse rugae anteriorly, punctures along midline polygonal, not distinctly circular (Fig. 26); midlobe of mesoscutum and entire scutellum with incomplete but regular cross-arcuate costae (Fig. 14), less distinct along scutellar sulcus, sidelobe of mesoscutum smooth anteriorly along notauli (black areas), laterally punctate-reticulate to rugose behind; apex of scutellum with distinctly or indistinctly septate marginal rim; scutellum slightly acuminate, sides convergent at about 75 degrees; underside of scutellum almost smooth (Fig. 40); median area of propodeum with deeply impressed foveae in form of distinct V-shape, submedian areas coriaceous above and smooth below with one or two transverse costae; postspiracular sclerite with very large fovea extended entire length of upper postspiracular sclerite (Fig. 30); axilla rugose; axillula smooth and shining, costae not extended to posterior border (Fig. 54).

*Metasoma*: T5 with indistinct punctures.

*Male*: Length, 3.7-4.6 mm. Color as in female except, dark violet area can extend along entire midlobe of mesoscutum and scutellum. Structure and sculpture as in female except: Head: Antennae: anellus relatively smaller, 0.15-0.23 length of F1; scape, in frontal view, expanded slightly apically, smooth, punctures indistinct and restricted to inner surface, outer surface with strong setae, surface roughened (Fig. 49). Mesosoma: Propodeum more coarsely sculptured with more prominent transverse costae. Genitalia (Fig. 75): digiti with three, four, or five large teeth and two smaller teeth; ventral lobe broadly rounded; lateral demelanized areas of basiparamere reduced laterally, pigmented median area shorter than digiti [ $n=4$ ].

*Variation*.— The Paraguayan specimen differs in a number of characteristics: sculpture of the midlobe of the mesoscutum is not reduced along the scutellar suture, and the axillula is not completely smooth but has a complete carina which parallels the ventral margin and defines a narrow finger-like region. This sculpture is different from that of *E. triangularis* which does not have a single carina but one to three oblique carinae (Fig. 53).

*Euperilampus enigma* n. sp.

(Figs. 50, 74)

*Type Locality*.— Bolivia, Santa Cruz, Roboré.

*Type Material*.— Holotype (Male, USNM No. 100318). Bolivia, Santa Cruz, Roboré (October 1959) [DCD Slide No. 73] [specimen donated to the USNM by UK]. See discussion under *E. brasiliensis* complex.

*Diagnosis*.— The holotype differs from all *E. brasiliensis* complex males by having large, recurved teeth on the digiti (Fig. 74; cf. Fig. 75, *E. brasiliensis* and Fig. 71, *E. luteicrus*). The distinct punctures on the anterior surface of the antennal scape (Fig. 50; cf. Fig. 49, *E. brasiliensis*), and the relatively large pronotum (PN:MSC=0.58) further distinguish the male of this species from those of *E. brasiliensis* [PN:MSC = 0.46-0.53]. There are fewer punctures on the scape than in *E. luteicrus* (Figs. 45, 46).

*Taxonomic note*.— A female specimen from Bolivia is tentatively associated with *E. enigma*: Female, Bolivia, Santa Cruz, Buena Vista (July 12 1971, Porter/Stange) [IML, identified as *Euperilampus triangularis* (Say) in Fidalgo 1980: 194; DCD Slide Nos. 135, 136, mouthparts, ovipositor]. This female is indistinguishable from *E. brasiliensis* and is not described.

*Derivation of specific epithet*.— From the Greek for 'something obscure, a riddle'; an allusion to the uncertain systematic affiliation of the holotype.

*Description*.—

*Male*: Length, 4.2 mm. Color predominantly blue-green, with violet reflections. Vertex, midlobe and sidelobe of mesoscutum with contrasting glossy black areas.

*Head*: Length of malar space 0.25 eye height; OOL = 0.87 POL; maximum width of scrobes 0.44 head width; margin of scrobes, in frontal view, sinuous, slightly flared at level of antennal toruli; head widest across eyes; head transverse, width:height = 1.17; inner orbital costae not convergent on posterior ocellus or extended around top of eye, ended abruptly at ocular-ocellar region (as in *E. brasiliensis*, Fig. 22); outer orbital costae short, largely confined to malar region; vertex almost smooth, posteriorly with transverse costae; clypeus transverse, width:height = 1.56, with indistinct arcuate costae at extreme lateral margins, punctures indistinct, surface appearing smooth and polished; supraclypeal area 0.52 clypeus height. Antennae: anellus 0.20 length of F1; scape, in frontal view, expanded slightly apically, length 4.53 times maximum width, with indistinct punctures on anterior and inner surfaces, outer surface with strong setae, surface roughened (Fig. 50).

*Mesosoma*: PN:MSC = 0.58; scutellum longer than mesoscutum, SC:MSC = 1.27; dorsum of pronotum punctate-reticulate, punctures coalesced in form of transverse rugae medially, punctures along midline polygonal, not distinctly circular; midlobe of mesoscutum and entire scutellum with incomplete but regular cross-arcuate costae (as in *E. brasiliensis*, Fig. 14), smooth along scutellar sulcus, sidelobe of mesoscutum with wide smooth area anteriorly along notauli (black areas), laterally punctate-reticulate to rugose behind; apex of scutellum with indistinctly septate marginal rim; scutellum slightly acuminate, sides convergent at about 75 degrees; underside of scutellum almost smooth (as in *E. brasiliensis*, Fig. 40); median area of propodeum with deeply impressed foveae in form of distinct V-shape, submedian areas distinctly coriarius with one or two transverse costae; postspiracular sclerite with very large fovea co-extensive with entire upper postspiracular sclerite; axilla rugose; axillula smooth and shining, costae not extended to posterior border (as

in *E. brasiliensis*, Fig. 54).

*Metasoma*: T5 with indistinct punctures. Genitalia (Fig. 74): digiti with three very large and three smaller teeth, teeth of right digitus recurved distally; ventral lobe broadly rounded; demelanized area of basiparamere large and quadrate, not reduced laterally, pigmented median area less than one-half length of digiti.

*Female*: UNKNOWN

*Euperilampus luteicrus* n. sp.

(Figs. 45, 46, 71)

*Type Locality*.— Mexico, Jalisco, Guadalajara.

*Type Material*.— Holotype (Male, USNM No. 100319): Mexico, Jalisco, 15 mi. NE Guadalajara (Sept. 17 1970, GE/RM Bohart) [DCD Slide No. 170, genitalia] [specimen donated to USNM by USU].

*Diagnosis*.— This holotype is the only New World specimen of *Euperilampus* with yellow fore and mid tibiae, concolorous with the tarsi. I expect the yellow tibiae will be diagnostic for the as yet unknown female. The antennal scape is covered with punctures (Figs. 45, 46), denser than in *E. enigma* (Fig. 50), and *E. brasiliensis* (Fig. 49). The scutellum is relatively longer than all other species in the *E. brasiliensis* complex, SC:MSC = 1.45, but the contrasting black areas on the sidelobe of the mesoscutum suggest affinities with *E. brasiliensis*.

*Geographical distribution*.— The type locality is in the Central Plateau region of México. Extent of range is unknown.

*Derivation of specific epithet*.— From the Latin (*luteus*, 'yellow' and *crus*, 'leg or shank'), with reference to the yellow fore and mid tibiae.

*Description*.—

*Male*: Length, 3.75 mm. Color predominantly blue-green, with violet reflections. Vertex, midlobe and sidelobe of mesoscutum with contrasting glossy black areas; fore and mid tibiae yellow, concolorous with tarsi.

*Head*: Length of malar space 0.25 eye height; OOL=POL; maximum width of scrobes 0.43 head width; margin of scrobes, in frontal view, sinuous, slightly flared at level of antennal toruli; head widest across eyes; head transverse, width:height = 1.19; inner orbital costae convergent on posterior ocellus, not extended around top of eye (as in *E. triangularis*, Fig. 21); outer orbital costae short, largely confined to malar region; vertex almost smooth, posteriorly with transverse costae; clypeus transverse, width:height = 1.60, with indistinct arcuate costae at extreme lateral margins, punctures indistinct, surface appearing smooth and polished; supraclypeal area 0.58 clypeus height. Antennae: anellus 0.12 length of F1; scape, in frontal view, expanded slightly apically, length 4.10 times maximum width, punctures dense and well developed on both anterior and inner surfaces, outer surface with strong setae, surface roughened (Figs. 45, 46).

*Mesosoma*: PN:MSC = 0.57; scutellum longer than mesoscutum, SC:MSC = 1.45, relatively longer than other *E. brasiliensis* complex species (range, 1.19-1.31); dorsum of pronotum punctate-reticulate, punctures coalesced in form of transverse rugae anteriorly, punctures along midline distinctly circular; midlobe of mesoscutum and entire scutellum with incomplete but regular cross-arcuate costae (as in *E. brasiliensis*, Fig. 14), smooth along scutellar sulcus, sidelobe of mesoscutum with wide smooth area anteriorly along notauli (black areas), laterally punctate-reticulate to rugose behind; apex of scutellum with distinctly septate marginal rim; scutellum slightly acuminate, sides convergent at about 75 degrees; underside of scutellum almost smooth; median area of propodeum with deeply impressed fovea in form of distinct V-shape, submedian areas smooth with few transverse costae and finer costulae; postspiracular sclerite with very large fovea co-extensive with entire upper postspiracular sclerite; axilla rugose; axillula smooth and shining, costae not extended to posterior border (as in *E. brasiliensis*, Fig. 54).

*Metasoma*: T5 with indistinct punctures. Genitalia (Fig. 71): digiti with three or four large teeth and two smaller teeth; ventral lobe broadly rounded; demelanized lateral areas of basiparamere large and oval, not reduced laterally, pigmented median area notched laterally and shorter than length of digiti.

*Female*: UNKNOWN

*Euperilampus ameca* n. sp.

*Type Locality*.— México, Nayarit, Santa Isabel.

*Type Material*.— Holotype (Female, USNM No. 100320): Mexico, Nayarit, 9 mi. NW Santa Isabella [= Isabel] (March 10 1972, Parker/Miller).

**Diagnosis.**— The holotype female differs from *E. brasiliensis* by having sidelobe of the mesoscutum almost completely sculptured and with the contrasting black areas very small and adjacent to the notauli. The short scutellum,  $SC:MSC = 1.30$ , establishes this species as a member of the *E. brasiliensis* complex.

**Geographical distribution.**— The type locality is in the Sierra Madre Occidental in the drainage of the Ameca River.

**Derivation of the specific epithet.**— A noun in apposition, from Ameca River.

**Description.**—

**Female:** Length, 5 mm. Color predominantly blue-green, with violet reflections. Vertex and midlobe of mesoscutum with contrasting glossy black areas, sidelobe of mesoscutum with black areas restricted to narrow band along anterior portion of notauli (much smaller than in other *E. brasiliensis* complex species).

**Head:** Length of malar space 0.29 eye height;  $OOL=0.94\ POL$ ; maximum width of scrobes 0.41 head width; margin of scrobes, in frontal view, sinuous and flared at level of antennal toruli (as in *E. triangularis*, Fig. 11); head widest across eyes; head transverse, width:height = 1.24; inner orbital costae not convergent on posterior ocellus or extended around top of eye, ended abruptly at ocular-ocellar region (as in *E. brasiliensis*, Fig. 22); outer orbital costae short, largely confined to malar region; vertex almost smooth, posteriorly with transverse costae; clypeus transverse, width:height = 1.59, with indistinct arcuate costae at extreme lateral margins, punctures indistinct, surface appearing smooth and polished; supraclypeal area 0.51 clypeus height. Antennae: anellus 0.25 length of F1; scape narrowly linear, length 4.53 times maximum width.

**Mesosoma:**  $PN:MSC = 0.43$ ; scutellum longer than mesoscutum,  $SC:MSC = 1.30$ ; dorsum of pronotum punctate-reticulate, punctures coalesced in form of transverse rugae medially, punctures along midline polygonal, not distinctly circular; midlobe of mesoscutum and entire scutellum with incomplete but regular cross-arcuate costae, sidelobe of mesoscutum without conspicuous smooth area anteriorly along notauli, this area roughened by indistinct rugae, laterally punctate-reticulate to rugose behind; apex of scutellum with distinctly septate marginal rim; scutellum slightly acuminate, sides convergent at about 75 degrees; underside of scutellum almost smooth (as in *E. brasiliensis*, Fig. 40); median area of propodeum with deeply impressed foveae in form of distinct V-shape, submedian areas coriaceous with single transverse costa dorsally; postspiracular sclerite with very large fovea co-extensive with entire upper postspiracular sclerite; axilla rugose; axillula smooth and shining, costae not extended to posterior border (as in *E. brasiliensis*, Fig. 54).

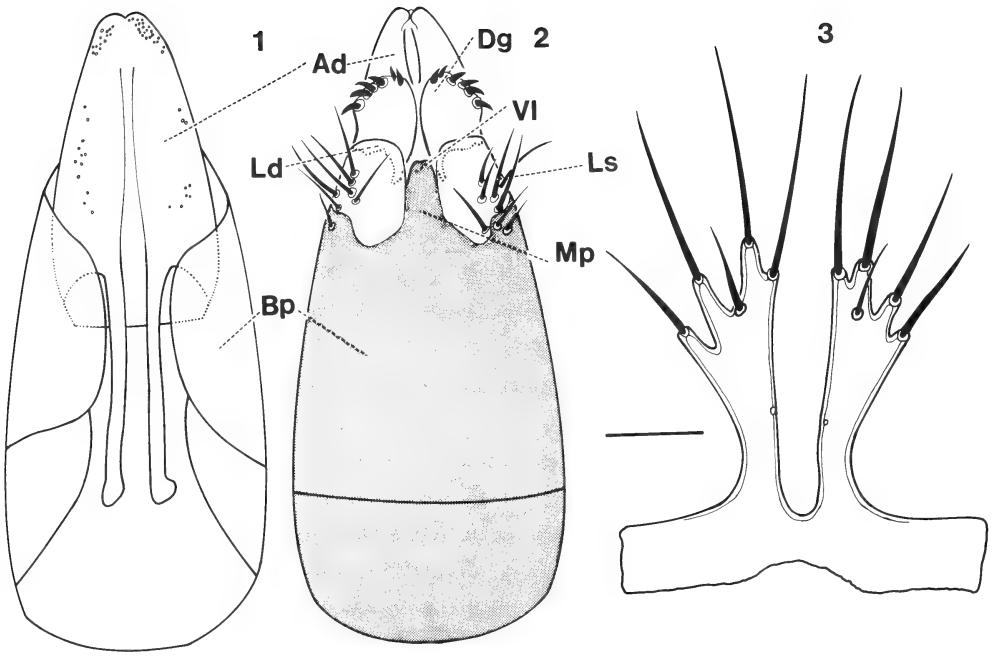
**Metasoma:** T5 with indistinct punctures.

**Male:** UNKNOWN

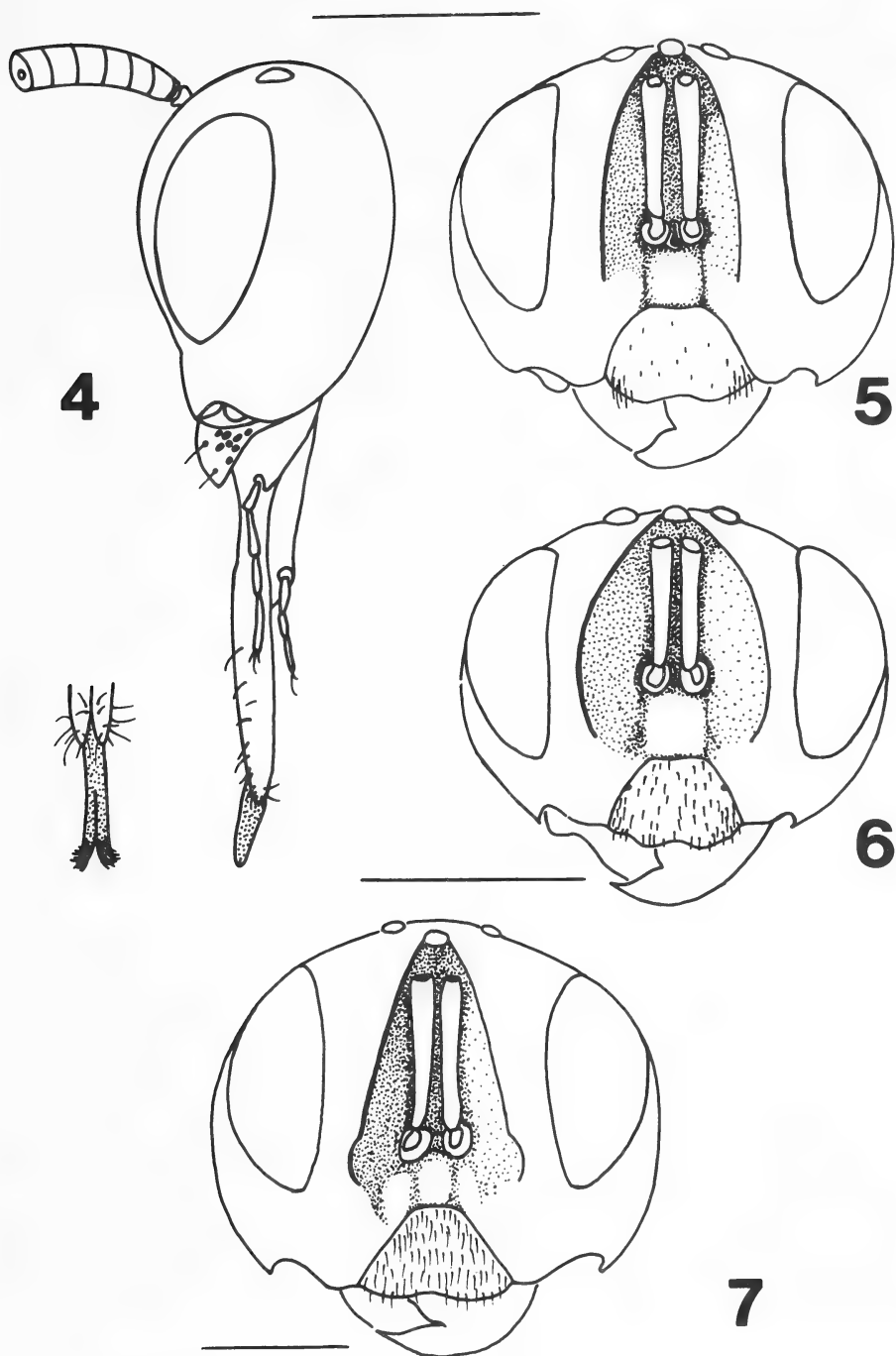


Table 1: Metric descriptors, for species of the *Euperilampus triangularis* species group, known from multiple specimens (see discussion of *E. triangularis* species group). Measurements as defined in 'Methods and Terms'. Diagnostic characters indicated by asterisk (\*). [ F, females; M, males.]

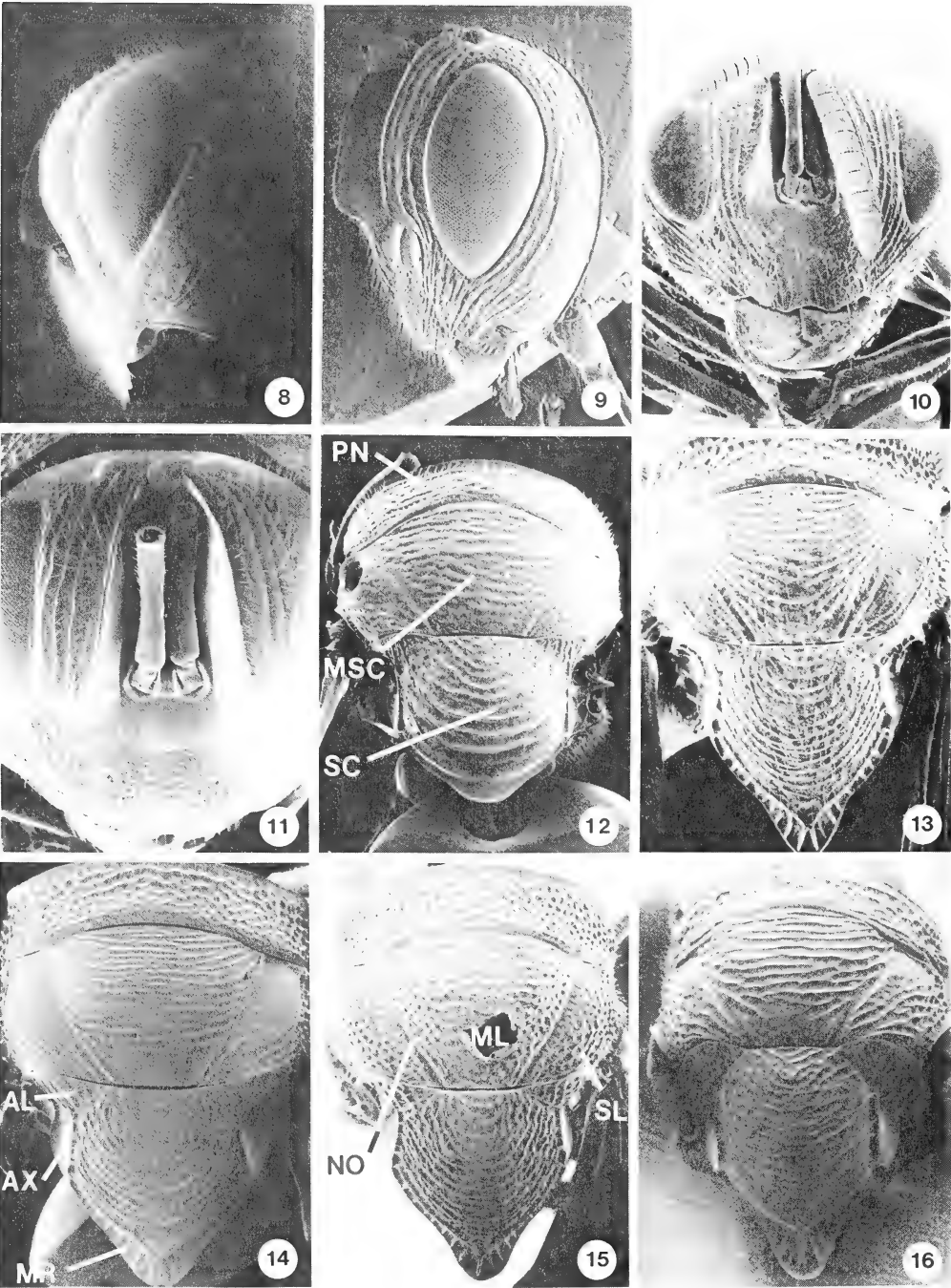
Character	<i>Euperilampus</i>			
	<i>iodes</i>	<i>solox</i>	<i>brasiliensis</i>	<i>triangularis</i>
MS/EH F	0.32-0.36	0.32-0.35	0.30-0.34	0.28-0.35
MS/EH M	0.30-0.33	0.28-0.31	0.23-0.24	0.22-0.29
*A/F1 F	0.27-0.32	0.26-0.35	0.25-0.33	0.18-0.25
*A/F1 M	0.14-0.25	0.21	0.15-0.23	0.10-0.15
SL/SW F	4.60-5.30	4.50-5.00	5.00-5.70	5.50-6.00
SL/SW M	4.00	4.20	4.30-4.80	3.80-4.20
PN/MSF F	0.30-0.41	0.42-0.47	0.40-0.46	0.34-0.44
PN/MSF M	0.43	0.46-0.50	0.46-0.53	0.35-0.48
*SC/MSF F	1.30-1.50	1.34-1.48	1.19-1.31	1.42-1.60
*SC/MSF M	1.36-1.43	1.43-1.50	1.24-1.31	1.42-1.75
HW/HL M & F	1.10-1.22	1.13-1.22	1.10-1.20	1.09-1.20
SH/CH M & F	0.44-0.55	0.46-0.59	0.45-0.52	0.41-0.52
CW/CH M & F	1.41-1.50	1.50-1.57	1.45-1.52	1.43-1.52
SW/HW M & F	0.38-0.40	0.41-0.43	0.37-0.44	0.41-0.47
OOL/POL M & F	1.00	0.79-1.03	0.68-0.94	0.70-1.00
# Males	2	2	4	18
# Females	7	5	12	17



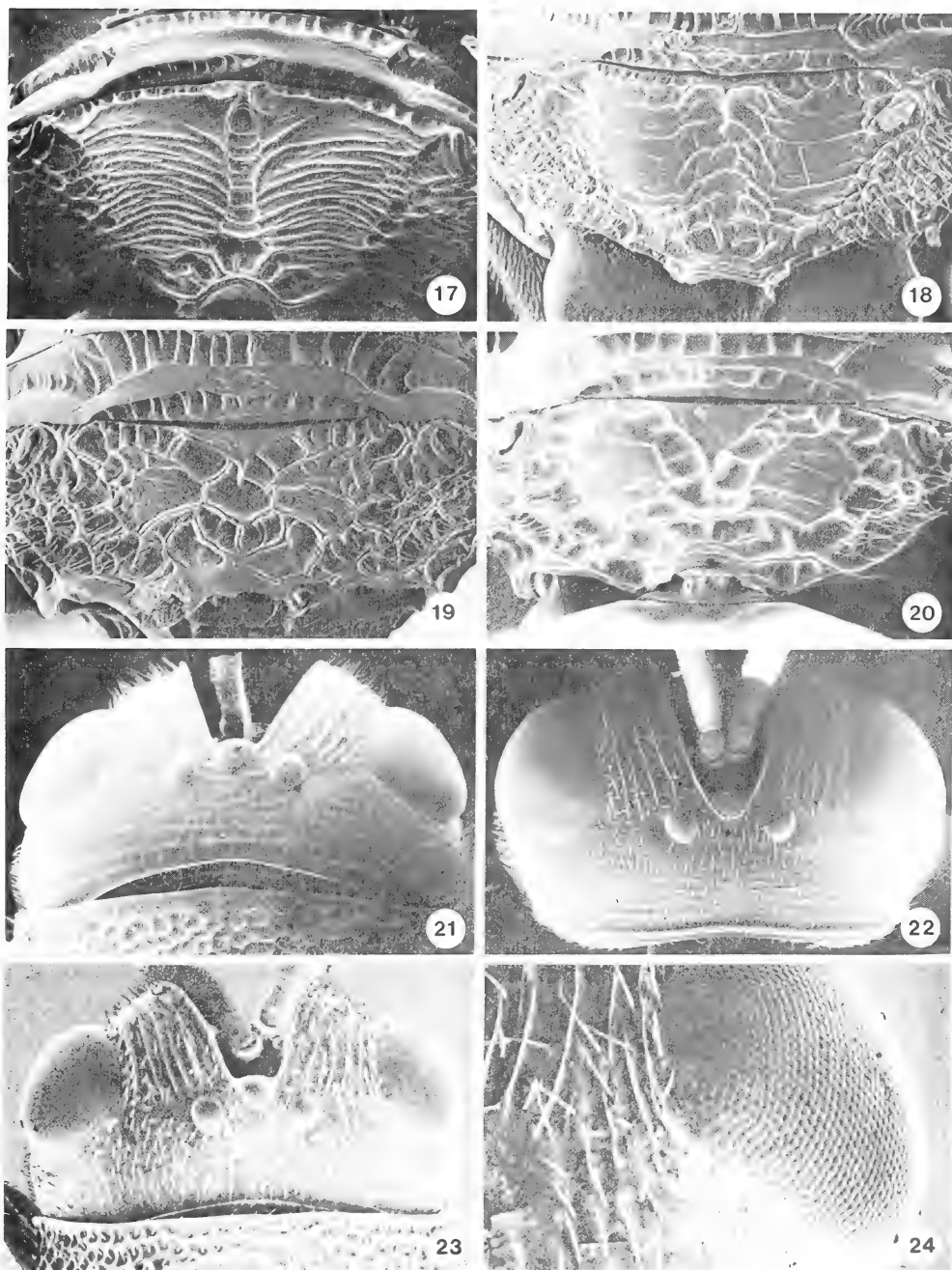
Figs. 1–3. Generic characters of *Euperilampus*. 1. Male genitalia *E. triangularis*, dorsal. 2. Male genitalia *E. triangularis*, ventral [ Ad, adeagus; Bp, basiparamere; Dg, digitus; Ld, lateral demelanized area of basiparamere; Ls, lateral setae; Mp, median pigmented area; VI, ventral lobe of basiparamere ]. 3. Labrum *E. triangularis*, dorsal view. Scale line 0.1 mm.



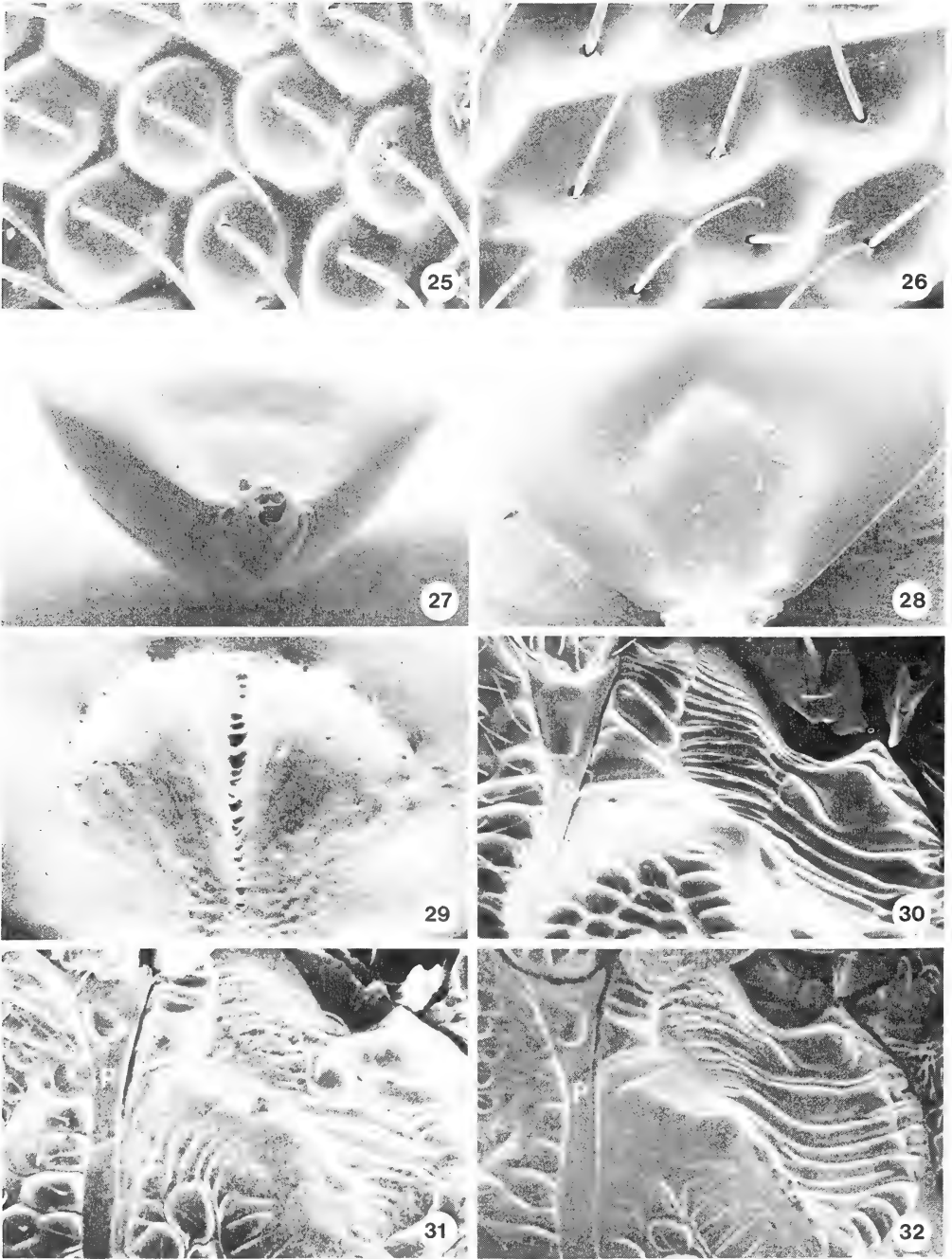
Figs. 4-7. Heads. 4. *E. tanyglossa*, female paratype; lateral. Inset; apex of labio-maxillary complex, anterior. 5. *E. tanyglossa*, female paratype; frontal. 6. *E. aureicornis*, female holotype; frontal. 7. *E. magnus*, female holotype; frontal. Scale line 1 mm.



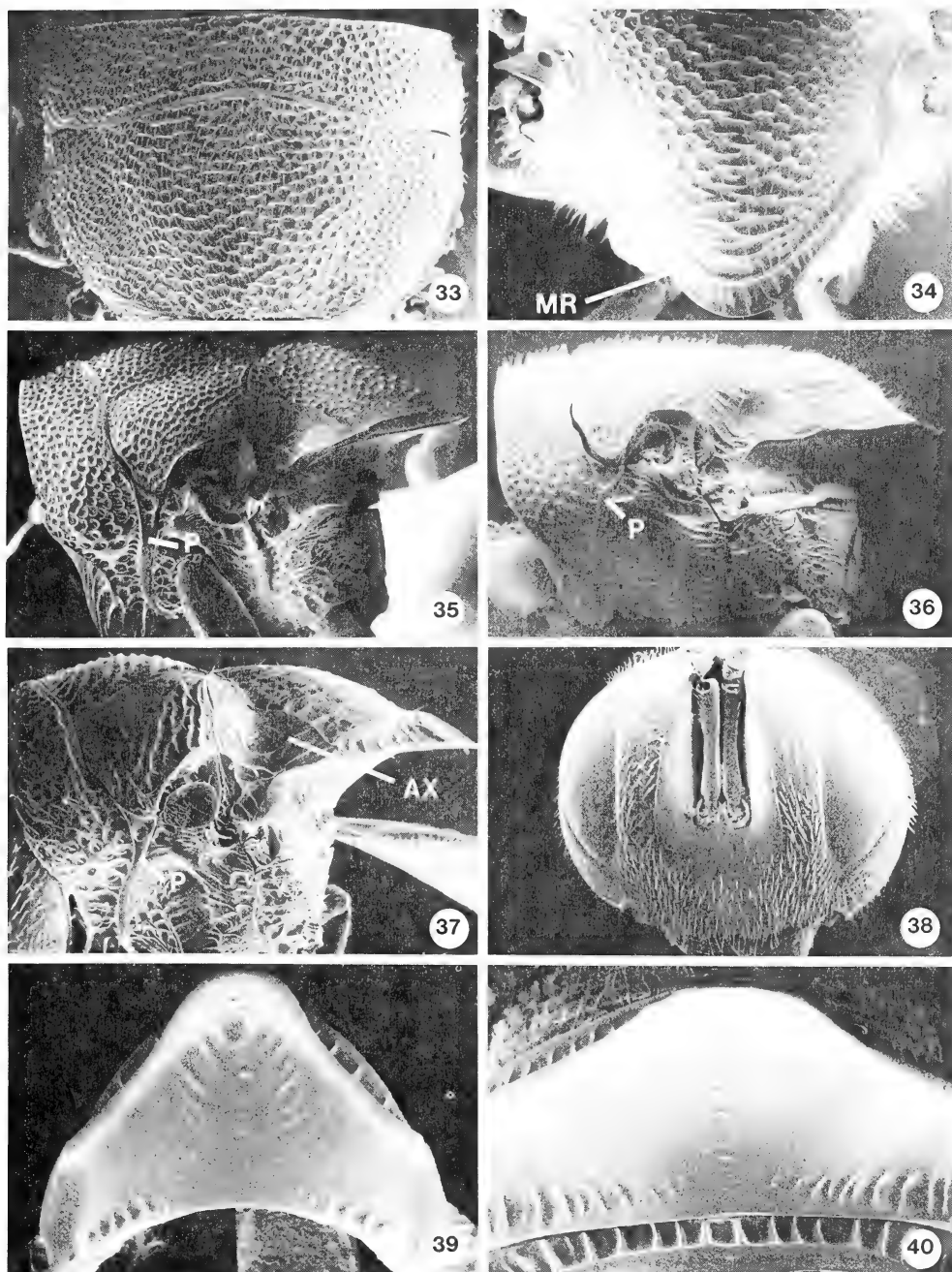
Figs. 8–16. 8–11. Heads. 8. *E. krombeini*; lateral. 9. *E. triangularis*; lateral. 10. *E. iodes*; frontal. 11. *E. triangularis*; frontal. 12–16. Mesosomata, dorsal. 12. *E. krombeini*. 13. *E. iodes*. 14. *E. brasiliensis*. 15. *E. solox*. 16. *E. triangularis* [AL, axilla; AX, axillula; ML, midlobe of mesoscutum; MR, marginal rim of scutellum; MSC, mesoscutum; NO, notaulex; PN, pronotum; SC, scutellum; SL, sidelobe of mesoscutum].



Figs. 17-24. 17-20. Propodea. 17. *E. krombeini*. 18. *E. tanyglossa*. 19. *E. triangularis*, Florida; length = 5.4 mm. 20. *E. triangularis* reared from *Hyposoter*, Arkansas, length = 2.9 mm. 21-24. Heads, dorsal. 21. *E. triangularis*. 22. *E. brasiliensis*. 23. *E. iodes*. 24. *E. iodes*; higher magnification, illustrating costae extending through ocular-ocular region along eye margin.

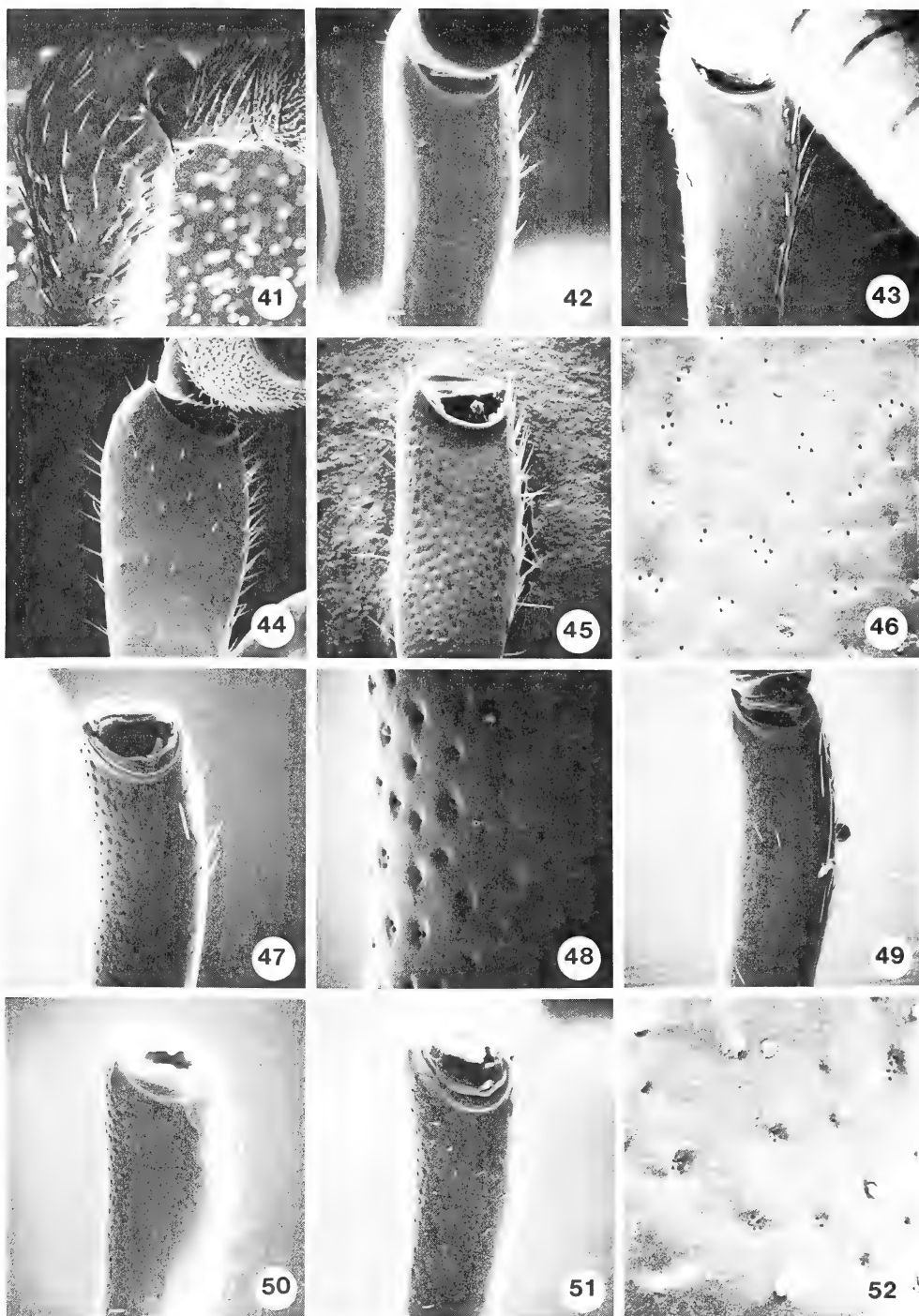


Figs. 25–32. 25–26. Sculpture types. 25. Punctate-reticulate, pronotum of *E. tanyglossa*. 26. Punctate-reticulate, punctures coalesced to form irregular rugae, pronotum of *E. brasiliensis*. 27–29. Second metasomal tergites. 27. *E. triangularis*. 28. *E. tanyglossa*. 29. *E. krombeini*. 30–32. Mesosomata, lateral. 30. *E. brasiliensis*. 31. *E. iodes*. 32. *E. solox* [P, postspiracular sclerite].



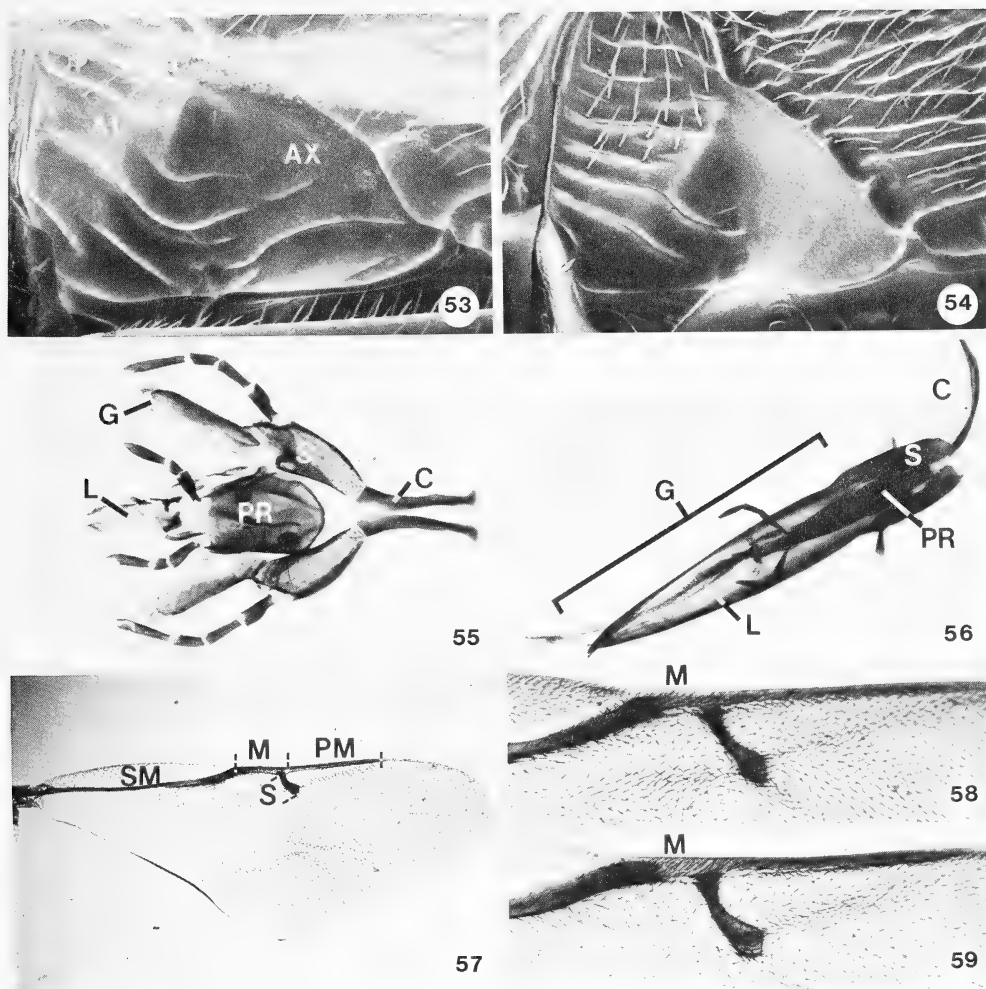
Figs. 33–40. 33–34. Mesosoma, *E. tanyglossa*. 33. Pronotum and mesoscutum, dorsal. 34. Scutellum, dorsal. 35–37. Mesosomata, lateral. 35. *E. tanyglossa*. 36. *E. krombeini*. 37. *E. triangularis*; 38. Head, frontal; *E. krombeini*. 39–40. Scutellum, underside. 39. *E. triangularis*. 40. *E. brasiliensis* [AX, axillula; MR, marginal rim of scutellum; P, postspiracular sclerite].



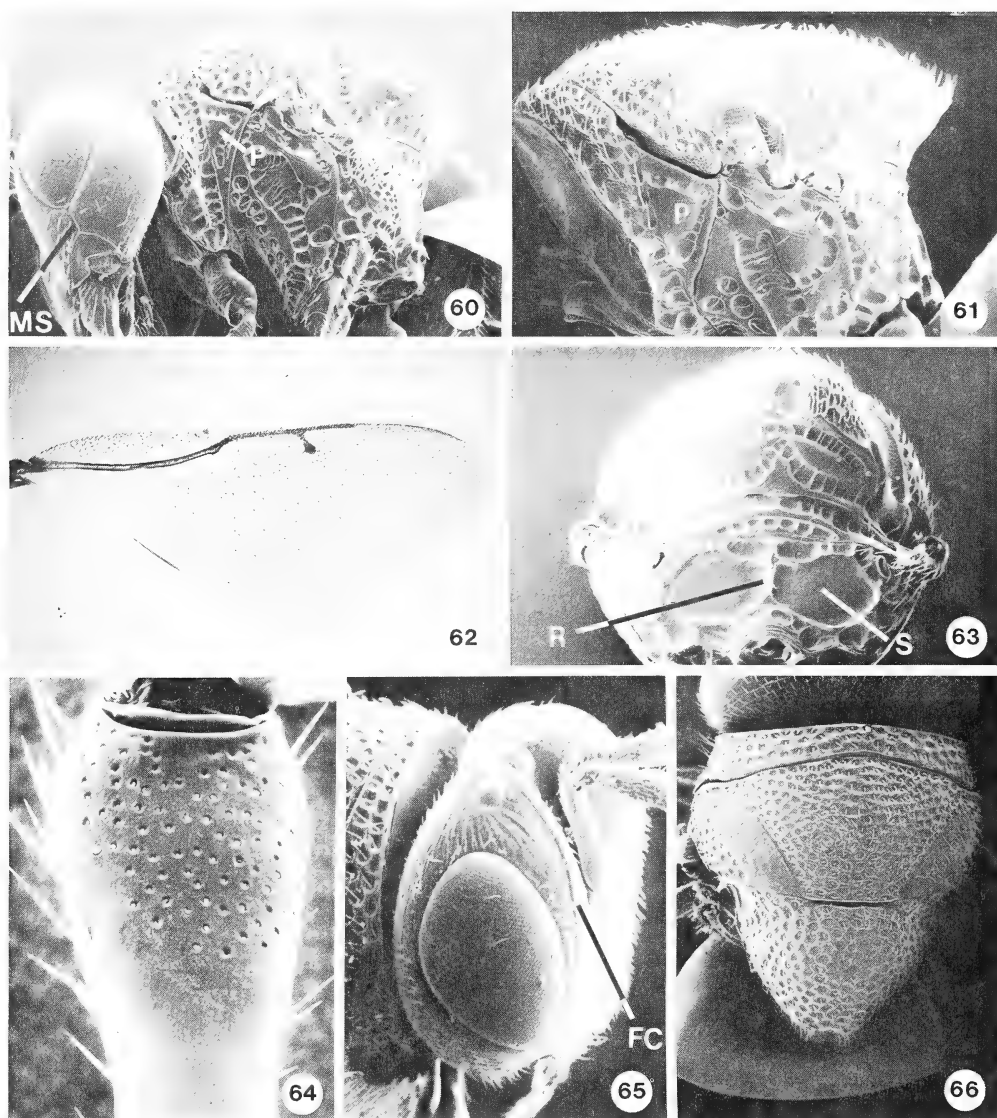


Figs. 41–52. Male antennal scapes. 41. *E. tanyglossa*, outer surface, 280x. 42–52. Anterior surfaces. 42. *E. tanyglossa*, 233x. 43. *E. krombeini*, 263x. 44. *E. triangularis*, 202x. 45. *E. luteicrus*, 233x. 46. *E. luteicrus*, 1,190x. 47. *E. solox*, 233x. 48. *E. solox*, 1,190x. 49. *E. brasiliensis*, 210x. 50. *E. enigma*, 233x. 51. *E. iodes*, 233x. 52. *E. iodes*, 1,190x.

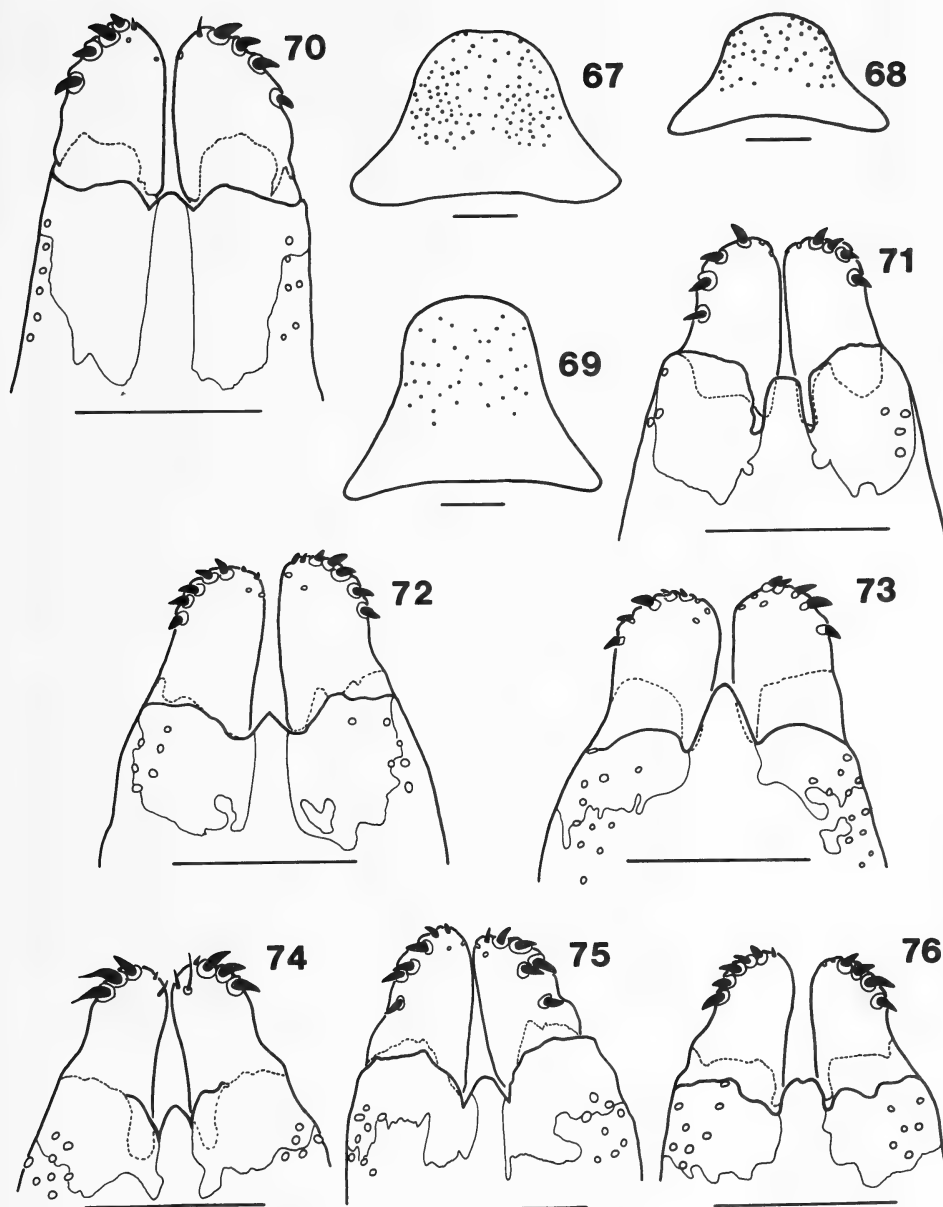




Figs. 53–59. 53–54. [AL, axilla; AX, axillula]. 53. *E. triangularis*. 54. *E. brasiliensis*. 55–56. Labio-maxillary complexes [C, cardo, S, stipes and G, galea or galea/lacinia of maxilla; PR, prementum; L, ligula of labium]. 55. *E. triangularis*. 56. *E. tanyglossa*. 57–59. Forewings. 57. *E. triangularis*. 58. *E. tanyglossa*. 59. *E. krombeini* [M, marginal, PM, postmarginal, S, stigmal and SM, submarginal veins].



Figs. 60–66. Character states in *Perilampus*. 60–61. Mesosomata, lateral. 60. *P. chysopae*. 61. *P. platygaster* [sic auct.]. 62. Forewing, *P. hyalinus*. 63. Propodeum, *P. platygaster*. 64. Male antennal scape, anterior surface, *P. hyalinus*. 65. Head, lateral, *P. hyalinus*. 66. Mesosoma, dorsal, *P. hyalinus* [FC, frontal carina; MS, malar sulcus; P, postspiracular sclerite; R, median ridge of propodeum; S, submedian area of propodium].



Figs. 67–76. Male genitalic structures of *Euperilampus*. 67–69. Subgenital plates. 67. *E. triangularis*. 68. *E. krombeini*. 69. *E. tanyglossa*. 70–76. Digits and apex of basiparamere, ventral view (compare with Fig. 2). The demelanized areas of the basiparamere are outlined and compared with the stippled areas in Fig. 2. The lateral setae (Ls) are not drawn. Scale line 0.1 mm. 70. *E. tanyglossa*. 71. *E. luteicrus*. 72. *E. iodes*. 73. *E. krombeini*. 74. *E. enigma*. 75. *E. brasiliensis*. 76. *E. solox*.

## PHYLOGENETIC RELATIONSHIPS

Hypotheses of phylogeny can be developed following the methods of Hennig (1966). Reference to an outgroup, ideally the sister group of the taxon under consideration, allows character states to be hypothesized as either plesiomorphic (ancestral) or apomorphic (derived). The degree of relationship, defined as the relative recency of common ancestry, can then be assessed based on shared derived characters (synapomorphies).

Character states and polarities are summarized in Table 2. The basis for the polarity decisions is outlined for the individual characters [ ] in the following discussion.

Intergeneric relationships within the Perilampidae are unresolved. All recognized genera show affinities with the speciose cosmopolitan genus *Perilampus* (Bouček 1978). It is quite possible that various species groups within *Perilampus* share a more recent common ancestor with other recognized genera than with other species of *Perilampus*.

A natural classification of the Perilampidae, i.e., one recognizing hypothesized phylogenetic relationships, must be based on recognition of monophyletic species groups within *Perilampus*. Smulyan (1936), in a revision of the nearctic species of *Perilampus*, recognized the 'carinate species group', based on possession of a distinct frontal carina (Fig. 65) and finger-like axillulae (Fig. 61). Both of these characters are here regarded as apomorphic in the Perilampidae. The frontal carina is absent from *Steffanolampus salicetum* (Steffan), and from species related to *Perilampus micans* Dalman [ groups I regard as early derivatives of *Perilampus* on the basis of the structure of the postspiracular sclerite and labrum]. The frontal carina is also absent from widely divergent species of *Perilampus*. However, in addition to the New World species of *Perilampus*, the frontal carina is also developed in Indo-Pacific species related to *P. punctiventris* Crawford (e.g., *P. singaporensis* Rohwer, *P. nesiotes* Crawford), and in *Krombeinius* and *Euperilampus*. The frontal carina [1] is here regarded as a synapomorphy uniting these groups.

Albeit inappropriately named, Smulyan's 'carinate group' is regarded as monophyletic on the basis of the finger-like axillulae; this character is only found in the New World carinate species and is therefore regarded as apomorphic. This group is perhaps better referred to as the '*Perilampus hyalinus* group', based on the widespread New World species.

The *Perilampus hyalinus* group shares an apomorphic character with species of *Krombeinius* and *Euperilampus*: the malar sulcus is obliterated by oblique striation (costae) [2], as noted by Bouček (1978:302).

*Krombeinius* and *Euperilampus* are united on the basis of the following synapomorphies: postspiracular sclerite reduced to a narrow triangle [3]; pronotum massive dorsally [12]; inner orbits with well developed raised costae or rugae [13] (characters noted by Bouček 1978); and the propodeum lacking a distinct median ridge [14]. The plesiomorphic states are found in all species of *Perilampus*; however, the raised costae on the inner orbits are slightly developed in some species of the *Perilampus hyalinus* complex.

*Euperilampus* is defined on the basis of the following apomorphies: male genitalia with reduced parameres [8]; labrum 8-digitate [11]; marginal vein shorter than postmarginal [5]; scutellum with a distinct marginal rim [9]; and metasomal T3 transverse, shorter than T2 [10]. Autapomorphies have yet to be documented for *Krombeinius*. The strikingly modified labrum (see under discussion of genus *Euperilampus*, examined in a single specimen) and the host association (primary parasites of solitary wasps, known only for the type species, *K. eumenidarum*; host: *Paraleptomenes mephitis* (Cameron)) are possibly autapomorphies.

The preceding hypotheses of relationships allow polarity determinations for character states found in *Euperilampus*. A character state is regarded as plesiomorphic in *Euperilampus* if it is present in *Krombeinius*. If both character states are present in *Krombeinius* then the state of the character in the *P. hyalinus* group is considered as plesiomorphic. A cladogram can then be constructed to show the distribution of derived character states.

I have extended the cladistic analysis only to species groups of *Euperilampus*. The New World species groups are as outlined in the 'Synopsis', and three terminal taxa are used in the analysis: *E. krombeini*, *E. tanyglossa* group and *E. triangularis* group. No attempt was made to present a cladogram of *E. triangularis* group species. The diagnostic characters are mainly sculpture and color differences. I expect considerable homoplasy in these characters (convergences and reversals), and hence the resultant cladogram would be suspect. Old World species are represented in the analysis by *E. mediterraneus* Bouček, and *E. scutellatus* (Girault). I have examined a long series of specimens of *E. scutellatus* [USNM]. *E. mediterraneus* is well illustrated and described (Bouček 1972), and character states can be determined. *E. hymenopterae* (Risbec), *E. beharae* (Risbec), *E. sinensis* Bouček and *E. spina* Bouček are not included in the analysis; for the characters listed in Table 2 these species appear to be identical with *E. scutellatus*.

*E. tanyglossa* group (*E. tanyglossa*, *E. aureicornis*) (both from México) and *E. mediterraneus* (southern Bulgaria) constitute a monophyletic group on the basis of the following synapomorphies: labio-maxillary complex elongate [20]; and stigmal vein longer than marginal vein [7]. The labio-maxillary complex is elongated in a similar way in *E. mediterraneus* (Bouček 1972, Fig. 2) and in the *E. tanyglossa* group: the galea/lacinia of maxilla and prementum, and ligula of the labium are greatly lengthened. The maxillary palps are also elongate in all three species. These similarities in detail suggest that this elaboration is homologous, and occurred only once, in the common ancestor of the *E. tanyglossa* group and *E. mediterraneus*. In *E. krombeini*, the stigmal vein is subequal in length to the marginal vein [6] (Fig. 59). This character state is phenotypically intermediate between the plesiomorphic and apomorphic states of character 7. I do not regard this as a linear transformation series or morphocline (stigmal vein shorter than marginal, stigmal vein equal to marginal, stigmal vein longer than marginal vein) on the basis of other characters. Seven synapomorphies indicate that *E. krombeini* and *E. mediterraneus* + *tanyglossa* group are not sister groups [4,15,17,22,18]. Only two characters support a sister group relationship between these taxa, and these are color characters [19,21], and are discussed later as convergences.

The long-tongued species of *Euperilampus* are united with *E. scutellatus* by the following characters: notauli indistinctly indicated [18]; and the mesoscutum uniformly sculptured, without a more weakly sculptured area along the notauli [22]. The alternative character states (see Table 2) are found in *Krombeinius* and *Perilampus* and therefore considered plesiomorphic for *Euperilampus*.

*E. triangularis* group and *E. krombeini* are united by the presence of cross-arcuate rugae or costae on the mesoscutum [17]; the deep median foveae on the propodeum [15]; and the postspiracular sclerite abruptly narrowed ventrally [4].

Figure 77 is the most parsimonious cladogram based on the characters in Table 2. This analysis is not free of homoplasy. Metallic colors [19] and infusate wings [21] appear to have arisen convergently in the two lineages of *Euperilampus*. It is interesting to note that all New World species have metallic colors and all Old World species are dark black. There is also a reversal indicated by this analysis. The raised costae on the inner orbits [13] are reduced in *E.*

Table 2: Polarity of character states in *Euperilampus* and related genera, based on outgroup comparisons (see text for discussion).

No.Attribute	Plesiomorphic State	Apomorphic State
1 Frontal carina	absent	present (Fig. 65)
2 Malar sulcus	distinct (Fig. 60)	obliterated by oblique costae (Fig. 9)
3 Width of postspiracular sclerite	as broad as adjacent pronotum (Figs. 60, 61)	reduced to narrow triangle, less than one-half as wide as the adjacent pronotum (Figs. 35-37)
4 Shape of postspiracular sclerite	gradually narrowed ventrally, not sinuous (Fig. 35)	abruptly narrowed ventrally, sinuous (Figs. 36, 37)
5 Marginal vein, forewing	longer than postmarginal (Fig. 62)	much shorter than postmarginal (Figs. 57-59)
6 Stigmal vein, forewing	much shorter than marginal (Fig. 57)	subequal to marginal (Fig. 59)
7 Stigmal vein, forewing	much shorter than marginal (Fig. 57)	longer than marginal (Fig. 58)
8 Parameres, male genitalia	distinct	reduced (Fig. 2)
9 Marginal rim of scutellum	absent (Fig. 66)	present (Fig. 34)
10 Metasoma, tergite 3	quadrate, much longer than T2	transverse, wider than long, shorter than T2
11 Labrum	10, 12 digitate	8 digitate (Fig. 3)
12 Pronotum, size	narrowed dorsally, much less than one-third length mesoscutum (Fig. 66)	massive, one-third to one-half length mesoscutum (Figs. 13-16)
13 Inner orbit sculpture	smooth or impunctate	with distinctly raised costae or rugae (Figs. 9-11)
14 Propodeum, sculpture	median area with distinct raised ridge (Fig. 63)	median area with foveae (Figs. 17-20)
15 Propodeum, sculpture	median area broad, with weak foveae, submedian areas not distinctly delimited (Fig. 18)	median area with distinct, deep foveae (Figs. 17,19,20)
16 Outer orbits	merge smoothly with face (Fig. 8)	merge abruptly with face (Fig. 9)
17 Mesoscutum, sculpture	punctate-reticulate (Fig. 33)	cross-arcuate rugae or costae (Fig. 14)
18 Notauli	distinct (Fig. 14)	indistinct (Fig. 33)

(continued on next page)

Table 2 (continued)

No.Attribute	Plesiomorphic state	Apomorphic state
19 Color	black	metallic violet to green
20 Labio-maxillary complex	short (Fig. 55)	elongate (Fig. 56)
21 Wing pigmentation	hyaline (Fig. 62)	infusate (Fig. 57-59)
22 Mesoscutum, sculpture	with slightly sculptured areas on the sidelobe (Fig. 14, 66)	evenly sculptured throughout (Fig. 33)

*krombeini*.

This preliminary analysis documents the monophyly of *E. tanyglossa* + *aureicornis* + *mediterraneus*; this relationship cannot be retrieved from a classification recognizing the subgenera *Euperilampus* (New World) and *Euperilampoides* (Old World). Further phylogenetic studies will be required for the placement of the remaining Old World species and should serve to test the present cladogram.

If the above hypothesized relationships of the *Perilampus hyalinus* group, *Krombeinius* and *Euperilampus* are corroborated by the placement of additional species, by additional characters, and the elucidation of monophyletic species groups within *Perilampus*, then the recognition of these two genera would render *Perilampus* paraphyletic. The genus would not include all species descended from a common ancestor. Species would be placed in *Perilampus* if they belonged to the Perilampidae but lacked the autapomorphies of the other genera. In the final analysis it may be prudent to retain *Krombeinius* and *Euperilampus* and to describe new genera, where needed, for monophyletic species groups of *Perilampus*. Clearly, the first priority for the development of a natural classification of the Perilampidae is the definition of monophyletic species groups within the core genus, *Perilampus*.

## ACKNOWLEDGEMENTS

I thank the following for comments on the manuscript: Z. Bouček, W. L. Brown, Jr., L. Burnham, J. M. Carpenter, G. C. Eickwort, G. A. P. Gibson, E. E. Grissell, N. F. Johnson, S. Nichols, M. J. Sharkey, M. Schauff, Q. D. Wheeler, and C. M. Yoshimoto.

The frontispiece was skillfully prepared by Jim Miller. Figures 10, 13, 15, 23, 24 and 31 were prepared from scanning electron micrographs of uncoated specimens; I thank H. F. Howden and L. E. C. Ling of Carleton University, Ottawa for these photographs.

This research was supported in part by a National Science Foundation Dissertation Improvement Grant. The Griswold Fund Committee, Department of Entomology, Cornell University assisted with the publication costs.

Special thanks are extended to Dr. J. G. Franclemont, for numerous discussions of all aspects of the project.

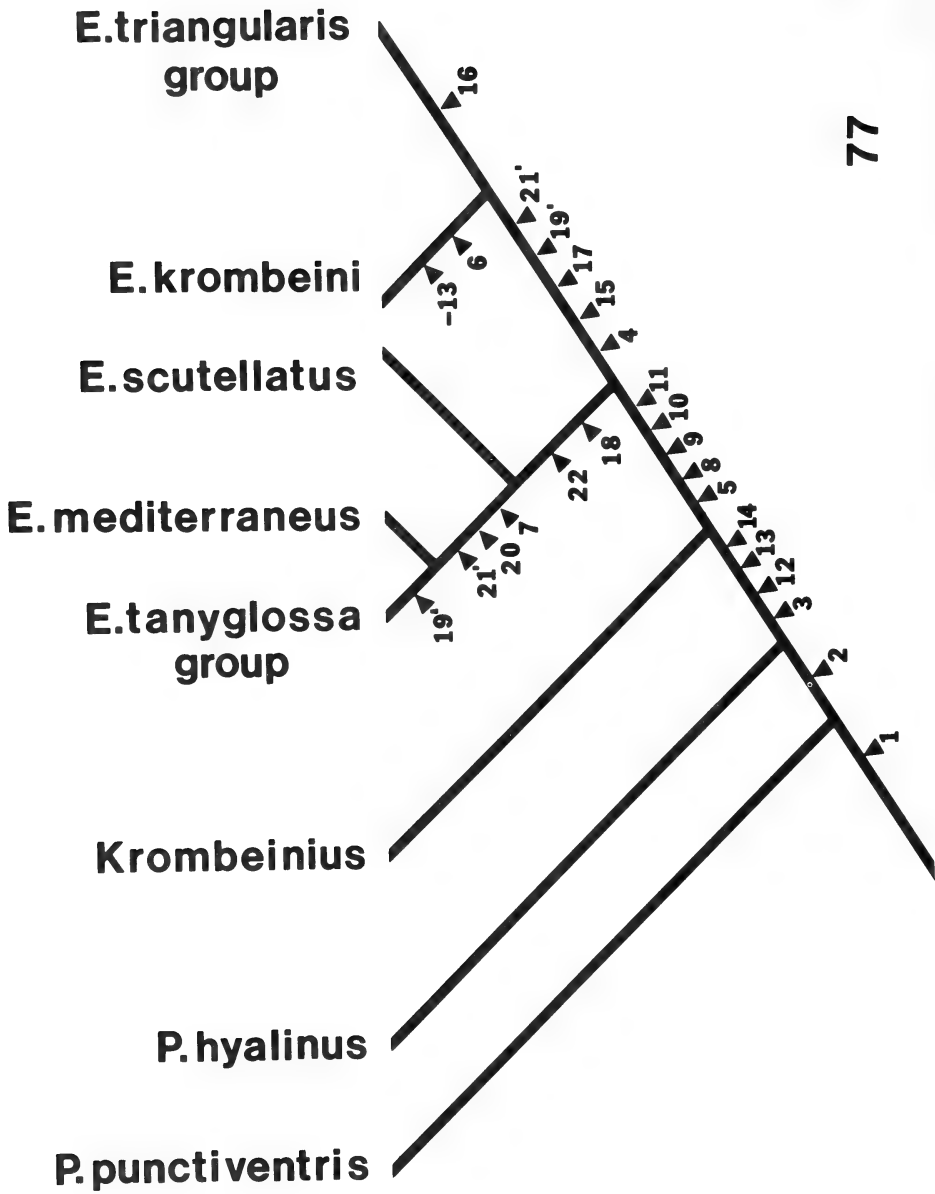


Fig. 77. Cladogram showing the distribution of shared derived characters (synapomorphies) in genera of Perilampidae and in species and species groups of *Euperilampus* (see text for discussion of species groups). x = synapomorphy, x' = convergence, -x = reversal. Autapomorphies of the terminal taxa are not presented. Characters are defined in Table 2.



## LITERATURE CITED

- Ashmead, W.H. 1890. On the Hymenoptera of Colorado. Bulletin of the Colorado Biological Association, 1. 46 pp.
- Ashmead, W.H. 1904. Classification of the Chalcid flies, or the Superfamily Chalcidoidea with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Memoirs of the Carnegie Museum 1(4): 225–251.
- Askew, R. R. 1980 (1979). The biology and larval morphology of *Chrysolampus thenae* (Walker) (Hym., Pteromalidae). The Entomologist's Monthly Magazine, 115: 155–159.
- Bouček, Z. 1972. Mediterranean Perilampinae: *Euperilampus* and genera allied to *Chrysomalla*. Mitteilungen der Münchener entomologischen Gesellschaft, 61: 90–107.
- Bouček, Z. 1978. A generic key to Perilampinae (Hymenoptera, Chalcidoidea), with a revision of *Krombeinius* n. gen. and *Euperilampus* Walker. Entomologica scandinavica 9: 299–307.
- Bouček, Z. 1980. A revision of the genus *Monacon* Waterston (Hymenoptera: Chalcidoidea: Perilampinae), parasites of ambrosia beetles (Coleoptera: Platypodidae). Bulletin of Entomological Research, 70: 73–96.
- Burks, B.D. 1969. New Perilampidae (Hymenoptera: Chalcidoidea). Proceedings of the Entomological Society of Washington, 71: 73–81.
- Burks, B.D. 1979. Family Pteromalidae, p. 768–835. In: Krombein, K.V., Hurd, P.D. Jr., Smith, D.R. and B.D. Burks. Catalog of Hymenoptera in America north of Mexico, Volume 1. Smithsonian Institution Press, Washington, D.C. 1198 pp.
- Clancy, D.W. 1946. The insect parasites of the Chrysopidae (Neuroptera). University of California Publications in Entomology, 7: 403–496.
- Crawford, J.C. 1914. The species of Perilampidae of America north of Mexico. Proceedings of the Entomological Society of Washington, 16: 69–76.
- Domenichini, G. 1953. Studio sulla morfologia dell'addome degli Hymenoptera Chalcidoidea. Bollettino di Zoologia Agraria e Bachicoltura, 19: 183–298, 27 Figs.
- Domenichini, G. 1969. Materiali per la morfologia comparata degli Hymenoptera Chalcidoidea. Memorie della Società Entomologica Italiana, 48: 584–608, 53 Figs.
- Eady, R.D. 1968. Some illustrations of microsculpture in the Hymenoptera. Proceedings of the Royal Entomological Society of London, (A): 43: 66–72, 31 Figs.
- Fidalgo, A.P. 1980. Neuvas citas de calcidoideos para Argentina, Bolivia y Peru (Hymenoptera). Neotropica, 26: 193–196.
- Fox, D.L. 1979. Biochromy. University of California Press, Berkeley. 248 pp.
- Girault, A.A. 1915. Australian Hymenoptera Chalcidoidea - V. Supplement. Memoirs of the Queensland Museum, 3: 300–312.
- Graham, M.W.R. de V. 1969. The Pteromalidae of north-western Europe (Hymenoptera: Chalcidoidea). Bulletin of the British Museum (Natural History) Entomology Supplement 16. 908 pp.
- Harris, R.A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, State of California, Department of Food and Agriculture, No. 28. 31 pp.
- Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, IL. 263 pp.
- Holland, W.J. 1919. Herbert Huntington Smith. Science, 49: 481–483.

- Parker, H.-L. 1924. Recherches sur les formes postembryonnaires des chalcidiens. Annales de la Société Entomologique de France, 93: 261-379.
- Peck, O. 1951. Superfamily Chalcidoidea, p. 410-594. In: Muesebeck, C.F.W., K.V. Krombein and H.K. Townes. Hymenoptera of America North of Mexico. Synoptic Catalog. U.S. Dept. Agr. Monogr. No. 2. 1420 pp.
- Peck, O. 1963. A catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). The Canadian Entomologist, Supplement 30. 1092 pp.
- Principi, M.M. 1947. Contributi allo studio dei Neurotteri Italiana V. Recherche su *Chrysopa formosa* Brauer e su alcuni suoi parassiti. Bollettino dell'Istituto di Entomologia della Università delgi studi di Bologna, 16: 134-175.
- Richards, O.W. 1977. Hymenoptera, Introduction and key to families, Second Edition. Royal Entomological Society of London, London. 100 pp.
- Riek, E. F. 1966. Australian Hymenoptera Chalcidoidea, Family Pteromalidae, Subfamily Perilampinae. The Australian Journal of Zoology, 14: 1207-1236.
- Rohwer, S.A. 1923. New Hymenoptera from the Malayan Region. The Philippines Journal of Science, 22: 345-353.
- Say, T. 1828. Descriptions of new species of Hymenoptera of the United States. Contributions of the Maclurian Lyceum of the Arts and Sciences, 1: 67-83.
- Smith, H.S. 1912. Technical results from the gypsy moth parasite laboratory. IV. The chalcidoid genus *Perilampus* and its relation to the problem of parasite introduction. United States Bureau of Entomology, Technical Series 19(4): 33-68.
- Smulyan, M.T. 1936. A revision of the chalcid flies of the genus *Perilampus* Latreille occurring in America north of Mexico. Proceedings of the United States National Museum, 83: 369-412.
- Walker, F. 1862. Notes on Chalcidites, and characterization of undescribed species. Transactions of the Entomological Society of London, (3)1: 345-397.
- Walker, F. 1871. Notes on Chalcidiae, Part IV. Chalcididae, Leucospidae, Agaonidae, Eucharidae, Perilampidae, Ormyridae, Eurytomidae. E. W. Janson, London. 129 pp.
- Warren, L.O. and M. Tadic. 1970. The fall webworm, *Hyphantria cunea* (Drury). University of Arkansas Agricultural Experiment Station Bulletin, 759. 106 pp.

# FILTER FEEDING OF *SIMULIUM FULVINOTUM* (DIPTERA: SIMULIIDAE) IN THE CENTRAL AMAZON BASIN

Lawrence A. Lacey<sup>1</sup>

Insects Affecting Man and Animals Research Laboratory

U. S. D. A., A.R.S., P.O. Box 14565

Gainesville, FL 32604

U.S.A.

Joyce M. Lacey

California Department of Water Resources

Northern District

2440 Main Street, P.O. Box 607

Red Bluff, CA 96080

*Quaestiones Entomologicae*

19: 41-51 1983

## ABSTRACT

*Filter feeding of larval Simulium fulvinotum Cerqueira and Mello was studied near Manaus, Brazil, using particulate fluorescent dye in small black water streams. Transit time of particles through the midgut was 29.2 min in one stream with a current velocity of ca. 1 m/sec and 0.37 mg/l seston, but was only 26.1 min in another stream with 1.5–2.0 m/sec velocity and 2.01 mg/l seston. Penultimate instars of S. fulvinotum held the cephalic fans open for an average of 3.3 min before they were closed for removal of particles. Food of larvae included a variety of algae, detritus, bacteria and insect parts. Methods for obtaining adequate nutrition in the habitats of S. fulvinotum are: less frequent cleaning of fans, an efficient filtering mechanism, and location of larvae in swift current.*

## RESUMO

*A alimentação através de filtração das larvas de Simulium fulvinotum Cerqueira e Mello foi estudada perto de Manaus, Brasil, utilizando uma tinta fluorescente em pequenos igarapês de água preta. O tempo de passagem através do intestino médio foi 29,2 min. em uma igarapé com correnteza de 1 m/seg e 0,37 mg/l de partículas em suspensão. Em outro igarapé com correnteza de 1,5–2,0 m/seg e 2,01 mg/l de partículas em suspensão, o tempo de passagem foi apenas 26,1 min. Indivíduos da penúltima etapa de S. fulvinotum mantiveram os filtros cefálicos abertos durante uma média de 3,3 min. antes de retrai-los para remover as partículas. A alimentação larval incluiu uma variedade de algas, detritos, bactérias e pedaços de insetos. As estratégias para obter nutrição adequada nos habitats de S. fulvinotum incluem movimentos mais lentos de alimentação, um mecanismo eficiente de filtração, e localização das larvas em correnteza rápida.*

Most biological research on the black flies of the Amazon Basin of Brazil has been on the adults of vector species with very little attention paid to the biology and ecology of larvae. One species which has been studied with respect to larval ecology and life history is *Simulium*

---

<sup>1</sup>Formerly with the Instituto Nacional de Pesquisas da Amazônia, Divisão de Ciências Médicas, Manaus, Brazil



Figure 1. Typical larval habitat of *Simulium fulvinotum*, Igarapé Acará Reserve Ducke, near Manaus, Brazil.

*fulvinotum* Cerqueira and Mello (1968); habitats were characterized by Dellome (1978); number of instars was determined by Gorayeb (1981); and predators of larvae were identified by Gorayeb and Pinger (1978).

Several studies have been conducted on the dynamics of filter feeding of other black fly species. Until now this aspect of the larval ecology of *S. fulvinotum* has not been investigated. In addition to providing basic information on the use of nutrients by simuliids in black water streams, information on larval feeding could also be useful when planning control of vector simuliid species in this habitat. Kershaw *et al.* (1968) and Helson and West (1978) demonstrated that particulate insecticides were active against target black flies with minimal effect on other aquatic organisms which did not filter feed. Feeding rate and retention time also will have a major influence on the efficacy of perorally active microbial control agents, such as *Bacillus thuringiensis* var. *israelensis* (Gaugler and Molloy 1980).

This paper presents information about filter feeding activity of larvae of *S. fulvinotum* in small streams near Manaus, Brazil.

### THE LARVAL HABITAT

*S. fulvinotum* larvae characteristically inhabit very swift current in small, shallow, black water streams (as defined by Sioli 1964; tannin-coloured, nutrient-poor water, draining podsols). The lip of the water drop in Figure 1 typifies the usual larval attachment site. In our study, habitats investigated were in primary and secondary forest 20–25 km northeast of Manaus, Brazil. In addition to typical larval habitats where current velocities of 1.5–2.0 m/sec (ca. 1 m<sup>3</sup>/sec discharge) were recorded, larvae were also found in one atypical stream (I) in current as low as 1 m/sec (.5 m<sup>3</sup>/sec discharge). Most streams where *S. fulvinotum* was found were heavily shaded. Stream I, however, was exposed to full sun because of recent deforestation.

Temperatures of 24.3–25.8°C and pH of 5.4–5.7 have been recorded for *S. fulvinotum* larval habitats (Cerqueira and Mello 1968, Dellome 1978). Water temperatures were 24.5–25.7°C during the course of our investigation.

### METHODS AND MATERIALS

Transit time of particles passing through the larval midgut was determined using a fluorescent dye (Hercules® Radiant Fluorescent Dye; orange WD 16).<sup>1</sup> Approximately 10 g of dye were suspended in a liter of water by vigorous shaking, then evenly poured into the river upstream of the larvae for 5–10 sec. After 10, 20, 30, and 40 min, leaves with attached larvae were carefully removed from the stream, so that larvae on adjacent leaves were not disturbed, and then stored in 70% ethanol. Ultimate larval instars were dissected to determine position of the dye plug in the midgut. Measurements of position of the dye and length of midgut were made with an ocular micrometer in a Zeiss dissecting microscope.

Gut filling times were recorded in Igarapé da Pedreira (Stream II) and Stream I. Both streams are located in the Cação Research Plantation (CEPLAC)) 25 km northeast of

---

<sup>1</sup>Mention of a commercial or proprietary product does not constitute an endorsement by the U.S.D.A.

Manaus. Temperature in each was measured with a mercury thermometer. Current velocity at the surface was determined using a float and stop watch. Suspended particles were measured by taking 3 one-litre samples of water from each site and individually vacuum filtering each through previously weighed millipore cellulose filters (0.45  $\mu$ m pores, 47 mm diameter filter at  $\leq 40$  cm Hg suction). The filters were then dried for 15 hrs at 65°C. After cooling and equilibrating for 6 hrs in the same conditions under which the original filter weights were taken, they were weighed on a Mettler H 34 balance ( $\pm 0.1$  mg accuracy).

Gut contents of late instars collected from Stream I on two separate occasions were analyzed. Larvae were placed on ice soon after collecting until they were dissected in the laboratory later in the same day. The dissected food columns were teased apart in distilled water and observed with the aid of a light microscope.

Feeding behaviour was observed in Stream I by viewing the larvae through the bottom of a 600 ml glass beaker which was lowered into the stream within a few centimetres of the attached larvae.

Data about transit time of particles through the midgut were analyzed with regression analysis (least squares method). The 20 min samples for the two streams were compared using Student's t-test.

Primary cephalic fans of ultimate instar *S. fulvinotum* (preserved in 70% ethanol) were prepared for scanning electron microscopy by: dehydrating in ethanol and freon; critical point drying in freon; and gold coating. Scanning electron micrographs were made with a Hitachi H-600 electron microscope.

## RESULTS

Mean quantities of suspended particles in Streams I and II were 0.37 and 2.01 mg/liter, respectively. Stream velocities were ca 1.0 and 1.5–2.0 m/sec respectively. Temperature in both streams was 25.2°C.

Table 1. Posterior displacement of dye plug in the midgut of *Simulium fulvinotum* in Stream I (suspended particles 0.37 mg/l; velocity 1.02 m/sec).

Min. after exposure	No. larvae	Mean % displacement $\pm$ S.E.*
10	17	38.18 $\pm$ 2.01
20	13	64.38 $\pm$ 2.73
30	11	103.0* $\pm$ 1.75

\*Calculated by position of dye in mid- and hindgut.

Table 2. Posterior displacement of dye plug in the midgut of *S. fulvinotum* in Stream II (suspended particles 2.01 mg/l; velocity 1.5–2.0 m/sec).

Min. after exposure	No. larvae	Mean % displacement $\pm$ S.E.
10	16	39.75 $\pm$ 3.17
20	30	77.23 $\pm$ 2.21
30	15	completely passed

Data used to determine time for particles to pass through midguts of *S. fulvinotum* larvae from Streams I and II are presented in Tables 1 and 2. Predicted transit times for the two streams were 29.2 and 26.1 min, respectively. Displacement of dye plugs 20 min after initial exposure in the two populations was significantly different ( $p < 0.05$ ). The mean for the 30 min sample from Stream I was calculated from the position of dye in both the mid- and hindguts of 11 larvae. The low variance in position of dye plugs observed in the 10 and 20 min samples in each of the streams indicates rather uniform feeding rates at each location.

Larvae observed feeding *in situ* held the cephalic fans open for an average of  $3.3 \pm .3$  min (range: 1.8–4.8;  $n = 10$ ). Fans were held closed for between 2 and 25 sec for removal of particles.

Analysis of gut contents revealed a high percentage of algae (more than 50%) and detritus. The various algal taxa represented were: Chlorophyta (*Oedogonium* sp., *Ankistrodesmus* sp., *Cosmarium* sp. and an unidentified filamentous species); Chrysophyta (*Melosira* spp., *Tabellaria* spp., *Fragilaria* sp., *Nitzschia* sp., and several genera of unidentified pennate diatoms); and Cyanophyta (*Chorococcus* sp., *Oscillatoria* sp., *Spirulina* sp., and an unidentified filamentous species). In addition to living diatoms, many empty diatom frustules were found. Also present were unidentified bacteria, insect parts and sand.

## DISCUSSION

The dynamics of filter feeding by black fly larvae have been elucidated by a number of investigators and summarized by Wallace and Merritt (1980). Particle transit times of from 20 min to more than 24 hr have been recorded (Davies and Syme 1958, Ladle, Bass and Jenkins 1972, Mulla and Lacey 1976, Elouard and Elsen 1977, Wotton 1978, Schröder 1980b). Differences in filtering activity and transit time of particles through guts of filter-feeding species may be due to species, instar, temperature, stream velocity, parasitism, imminent pupation, and amount and dimensions of available seston (Mulla and Lacey 1976, Chance 1977, Elouard and Elsen 1977, Moore 1977b, Elsen, Quillévére and Hebrard 1978, Wotton 1978, Elsen and Hebrard 1979, Lacey and Mulla 1979, Elsen 1980, Schröder 1980 a, b). Increased stream velocity and/or additional amount of suspended matter in Stream II was responsible for the accelerated feeding rate of *S. fulvinotum* over that observed in Stream I. An even greater difference in feeding rate might be expected based on disparity of seston concentration and stream velocity between Streams I and II. Lack of exaggerated differences might be explained as a function of the inherent maximum filtering efficiency of *S. fulvinotum*. Kurtak (1978) observed a decrease in filtering efficiency (i.e., the portion of particles ingested

per larva per second relative to the total number of particles offered per fan area per second) when concentration of particles and stream velocity increased. Under laboratory conditions, Lacey and Mulla (1979) and Schröder (1980b) reported plateaus of optimal particle concentration and stream velocity for maximum ingestion rates. Beyond the optimum range, an increase in current velocity and particle concentration may result in feeding inhibition (Lacey and Mulla 1979, Gaugler and Molloy 1980).

A few ultimate instars with dark histoblasts (pharate pupae) were observed without dye plugs and with partially or completely empty midguts. Feeding had apparently ceased prior to pupation, and the gut was emptied by peristaltic action. Chance (1977) reported that *Simulium vittatum* Zetterstedt larvae may refrain from feeding for periods of 90 min or longer. In our study, the only individuals which failed to filter dye were pharate pupae.

Choice of larval habitat appears to be related to specific feeding methods for several black fly species (Carlsson *et al.* 1977, Kovachev 1979, Wotton 1979, 1980b) or at least choice of a specific habitat markedly influences type of nutrient the larvae will encounter (Maciolek and Tunzi 1968, Kurtak 1979). Selection of a habitat with an optimally high stream velocity would appear to maximize feeding rates where seston levels are as low as those found in the black water streams inhabited by *S. fulvinotum* larvae. In streams with waterfalls or other zones of very swift current, *S. fulvinotum* larvae are invariably found in the fastest current. Initial selection of these sites is apparently made by the ovipositing female (Gorayeb 1981).

Other feeding methods that would enhance ingestion would be more efficient use of the filtering mechanism and behaviour. Simuliid larvae are capable of filtering colloidal sized particles (Wotton 1976). Capture of these and other particles smaller than the spaces between the microtrichia of the cephalic fan rays is apparently aided by a mucosubstance which coats the cephalic fans (Ross and Craig 1980). A single median ray of the primary cephalic fan of *S. fulvinotum* is shown in Fig. 2. An enlargement of the middle portion of the ray (Fig. 3) shows microtrichia used for capture of fine particles. Microtrichia of *S. fulvinotum* are considerably longer than those of *S. vittatum* (D. A. Craig, personal communication), a species found in streams with moderate to high seston concentrations. Accelerated feeding rate of *S. fulvinotum* is at least partially influenced by this morphological adaptation to low seston loads. Increased surface area of the filtration mechanism of *S. fulvinotum* probably facilitates capture of a greater number of particles per unit of time.

Time spent by *S. fulvinotum* larvae with fans open is considerably greater than that reported by Kurtak (1973) and Craig and Chance (1982) for *S. vittatum*. Ostensibly *S. fulvinotum* maximizes contact of its cephalic fans with the current in compensation for a low particulate load. Craig and Chance (1982) hypothesize that larvae with less frequent mouthpart movements may filter more efficiently than those which clean their fans more often because the latter have their fans adducted (not exposed to food) for a significantly greater period of time. Rapid flicking of fans reported by other investigators was only occasionally seen during our observations. Observations were only made in Stream I because of disturbance of larvae in Stream II when they were observed from upstream. Observations from downstream were not possible because of a 2.5 m waterfall.

Gut contents of filter-feeding black fly larvae generally reflect relative abundance of nutritional materials within a particle size range that they can filter in the stream where they are located (Maciolek and Tunzi 1968, Moore 1977a, b, Wotton 1977, Kurtak 1979, Wallace and Merritt 1980). A wide variety of food types has been recorded for simuliid larvae, ranging from animal matter (Serra-Tosio 1967, Burton 1971, Disney 1971) to algae (Anderson and



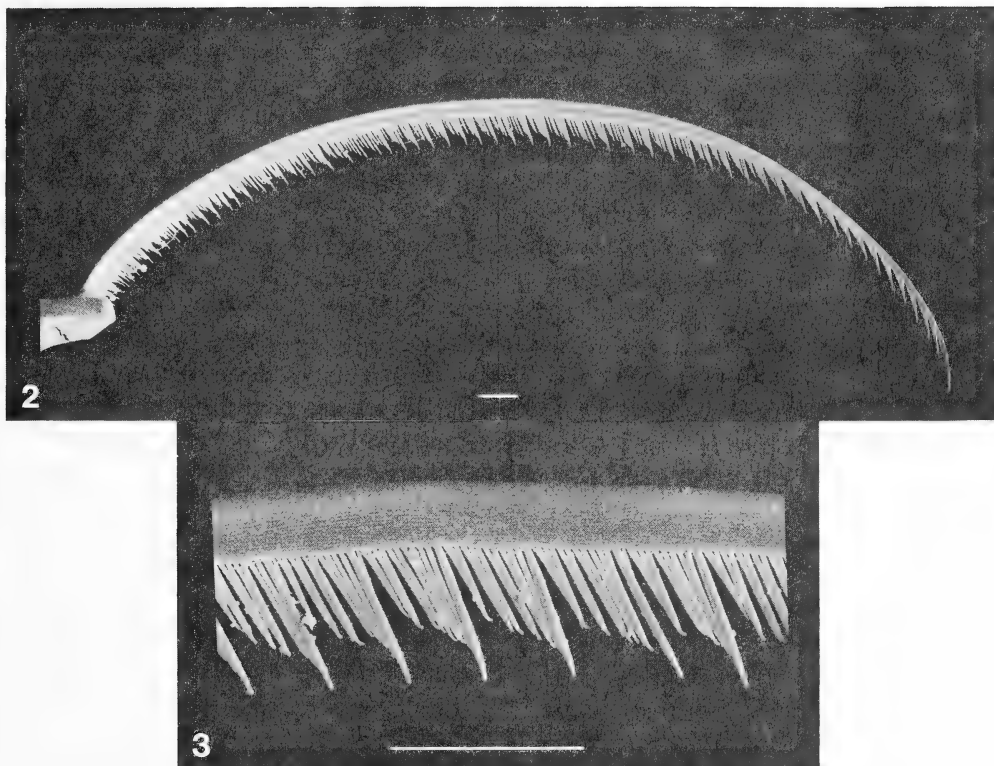


Figure 2. Middle ray of primary cephalic fan of *Simulium fulvinotum* larva.

Figure 3. Median portion of middle ray in Figure 2. Scale = 20  $\mu$ m.

Dicke 1960, Maitland and Penney 1967, Burton 1973, Pavlichenko *et al.* 1977), bacteria (Fredeen 1964, Pavlichenko *et al.* 1977, Wotton 1980a) and detritus (Cummins and Klug 1979). Considering the low seston load, it was interesting to find algae making up the major portion of the diet of *S. fulvinotum* larvae. Algae in streams are characteristically benthic, so their contribution to the seston is generally considered to be accidental (Whitton 1975). Scraping of the substrate by *S. fulvinotum* larvae may account for the high proportion of algae in the gut. It is possible that this activity was not observed because of the low number of observations that were made *in situ*. Mokry (1975) reported that in an "average" hour, *Simulium venustum* larvae scraped for 20 min, filtered for 20 min, and rested for 20 min. Some investigators have questioned nutritional value of living algae and recently dead plant matter to larvae which have a relatively brief retention time. Kurtak (1979) and McCullough *et al.* (1979), however, reported that more than 50% of ingested diatoms were digested. Similar findings were reported by Maciolek and Tunzi (1968). In our research, the large number of empty frustules may be an indication of digestion.

Although bacteria did not appear to be a major source of food in our samples, they may be a necessary component for detritus use through biochemical alterations of the detrital substrate (Cummins and Klug 1979). Alternatively, Anderson and Cummins (1979) suggest that since retention time of food in the gut is so brief in larval simuliids, bacteria stripped from the surface of refractory detritus particles probably contribute most of the nutritional value. Lotic food sources of simuliids and their relationship with microbes are summarized by Cummins and Klug (1979).

Abundant detritus in the form of fine particulate organic matter has been associated with maintenance of dense populations of simuliid larvae (Carlsson *et al.* 1977, and other authors cited by Anderson and Seddell 1979). Detritus may have varying degrees of importance in the diet of *S. fulvinotum* larvae depending on season, location and deforestation activity. As was previously stated, most sites for *S. fulvinotum* were found under dense canopy. The site where larvae were collected for analysis of gut content was exposed to sunlight and was undoubtedly more conducive to a higher proportion of algae in the water and on the substratum. Kurtak (1979) reported variability in percentage of various food types in streams in which he worked both as a function of season and location.

The ecological role of black fly larvae, at times the most abundant aquatic insect in small streams of the Central Amazon, requires further elucidation. Areas for future research could include production studies on the larvae of *S. fulvinotum* in a wider variety of locations and seasons as well as comparison with other species of simuliids in the same general habitat. Research on the range of particle sizes ingested would be a useful first step in studying the effects of particulate insecticides on black fly larvae and nontarget organisms in the habitat of *S. fulvinotum*.

Due to its ubiquity and accessibility, *S. fulvinotum* will provide an excellent model for the study of nutrient utilization and cycling and insecticide use in the nutrient-poor black water environment.

#### ACKNOWLEDGEMENTS

The helpful comments and advice of Roger Wotton, Goldsmith's College, University of London, Douglas A. Craig, University of Alberta, and Albert Undeen, U.S.D.A., during the preparation of the manuscript are very much appreciated. We are also grateful to D. A. Craig

for making the scanning electron micrographs.

## REFERENCES

- Anderson, J. R. and R. J. Dicke. 1960. Ecology of the immature stages of some Wisconsin black flies (Simuliidae: Diptera). *Annals of the Entomological Society of America* 53: 386–404.
- Anderson, N. H. and K. W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36: 335–342.
- Anderson, N. H. and J. R. Sedell. 1979. Detritus processing by macro-invertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351–377.
- Burton, G. J. 1971. Cannibalism among *Simulium damnosum* (Simuliidae) larvae. *Mosquito News* 31: 602–603.
- Burton, G. J. 1973. Feeding of *Simulium hargreavesi* Gibbons larvae on *Oedogonium* algal filaments in Ghana. *Journal of Medical Entomology* 10: 101–106.
- Carlsson, M., M. Nilsson, Bj. Svensson, S. Ulfstrand, and R. S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. *Oikos* 29: 229–238.
- Cerqueira, N. L. and J. A. N. Mello. 1968. Simuliidae da Amazônia. IV. Descrição de *Simulium fulvinotum* sp. n. (Diptera, Nematocera). *Amazoniana* 1: 205–210.
- Chance, M. M. 1977. Influence of water flow and particle concentration on larvae of the black fly *Simulium vittatum* Zett. (Diptera: Simuliidae), with emphasis on larval filter feeding. Ph. D. dissertation. University of Alberta.
- Craig, D. A. and M. M. Chance. 1982. Filter-feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydro-dynamics. *Canadian Journal of Zoology* 60: 712–724.
- Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147–172.
- Davies, D. M. and P. D. Syme. 1958. Three new Ontario black flies of the genus *Prosimulium* (Diptera: Simuliidae) Part II. Ecological observations and experiments. *Canadian Entomologist* 90: 744–759.
- Dellome, J. 1978. Fatores físicos-químicos das criadouros de Simuliidae (Diptera: Nematocera). Master's thesis. Instituto Nacional de Pesquisas da Amazônia and Fundação Universidade do Amazonas, Manaus, Brazil.
- Disney, R. H. L. 1971. Association between black flies (Simuliidae) and prawns (Atyidae), with a discussion of the phoretic habit in Simuliids. *Journal of Animal Ecology* 40: 83–92.
- Elsen, P. 1980. Le transit intestinal chez les larves du complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. III. Influence du stade larvaire, du nycthemere et de la saison. *Annales de la Société belge Médecine tropicale* 60: 203–213.
- Elsen, P. and G. Hebrard. 1979. Le transit intestinal chez les larves du complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. II. Influence de la température de l'eau, de la concentration de particules et de la nature de ces particules. *Ibid* 59: 49–58.
- Elsen, P., D. Quillévéré, and G. Hebrard. 1978. Le transit intestinal chez les larves du

- complexe *Simulium damnosum* (Diptera, Simuliidae) en Afrique de l'Ouest. 1. Influence de sexe et de l'espèce. *Ibid* 58: 209–217.
- Elouard, J.-M. and P. Elsen. 1977. Variations de l'absorption de particules alimentaires et de la vitesse de transit digestif en fonction de certains paramètres du milieu chez les larves de *Simulium damnosum* Theobald 1903 (Diptera, Simuliidae). Cah. O.R.S.T.O.M. ser. Ent. Méd. et Parasitol 15: 29–39.
- Fredeen, F. J. H. 1964. Bacteria as food for black fly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Canadian Journal of Zoology 42: 527–554.
- Gaugler, R. and D. Molloy. 1980. Feeding inhibition in black fly larvae (Diptera: Simuliidae) and its effects on the pathogenicity of *Bacillus thuringiensis* var. israelensis. Environmental Entomology 9: 704–708.
- Gorayeb, I. S. 1981. Comportamento de oviposição e ciclo evolutivo de *Simulium fulvotum* Cerq. e Mello 1968 (Diptera, Nematocera). Acta Amazônica 11: 595–604.
- Gorayeb, I.S. and R.R. Pinger. 1978. Detecção de predadores naturais das larvas de *Simulium fulvotum* Cerq. e Mello, 1968 (Diptera, Nematocera). *Ibid.* 8: 629–637.
- Helson, B. V. and A. S. West. 1978. Particulate formulations of Abate® and methoxychlor as black fly larvicides: their selective effects on stream fauna. Canadian Entomologist 110: 591–602.
- Kershaw, W. E., T. R. Williams, S. Frost, R. E. Matchett, M. L. Mills, and R. D. Johnson. 1968. The selective control of *Simulium* larvae by paraticulate insecticides and its significance in river management. Transactions of the Royal Society of Tropical Medicine and Hygiene 62: 35–40.
- Kovachev, S. 1979. Saprobic sequences within the family Simuliidae and their importance for water quality assessment. Hydrobiology (Sofia) 9: 50–56. (In Bulgarian with Russian and English Summaries).
- Kurtak, D. C. 1973. Observations on filter feeding by the larvae of black flies (Diptera: Simuliidae). Ph. D. dissertation. Cornell University. 172 pp.
- Kurtak, D. C. 1978. Efficiency of filter feeding of black fly larvae (Diptera: Simuliidae). Canadian Journal of Zoology 56: 1608–1623.
- Kurtak, D. C. 1979. Food of black fly larvae (Diptera: Simuliidae): seasonal changes in gut contents and suspended material at several sites in a single watershed. Quaestiones Entomologicae 15: 357–374.
- Lacey, L. A. and M. S. Mulla. 1979. Factors affecting feeding rates of blackfly larvae (Diptera: Simuliidae). Mosquito News 39: 315–319.
- Ladle, M., J. A. B. Bass, and W. R. Jenkins. 1972. Studies on production and food consumption by the larval Simuliidae (Diptera) of a chalk stream. Hydrobiologia 39: 429–448.
- Maciolek, J. A. and M. G. Tunzi. 1968. Microseston dynamics in a simple Sierra Nevada lake-system. Ecology 49: 60–75.
- Maitland, P. S. and M. M. Penney. 1967. The ecology of the Simuliidae in a Scottish river. Journal of Animal Ecology 36: 179–206.
- McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. Ecology 60: 585–596.
- Morky, J. E. 1975. Studies on the ecology and biology of blackfly larvae utilizing an *in situ* benthobiosurvey. Verh. Internationale Vereinigung für Limnologie 19: 1546–1549.

- Moore, J. W. 1977a. Relative availability and utilization of algae in two subarctic rivers. *Hydrobiologia* 54: 201–208.
- Moore, J. W. 1977b. Some factors affecting algal consumption in subarctic Ephemeroptera, Plecoptera, and Simuliidae. *Oecologia* 27: 261–273.
- Mulla, M. S. and L. A. Lacey. 1976. Feeding rates of *Simulium* larvae on particulates in natural streams (Diptera: Simuliidae). *Environmental Entomology* 5: 283–287.
- Pavlichenko, V. I., A. K. Shehvenko, and M. V. Steblyuk. 1977. Study of the food spectrum of black fly larvae Diptera, Simuliidae. *Vestn. Zool* 1: 64–68. (In Russian with English summary).
- Ross, D. H. and D. A. Craig. 1980. Mechanisms of fine particle capture by larval black flies (Diptera: Simuliidae). *Canadian Journal of Zoology* 58: 1186–1192.
- Schröder, P. 1980a. Zur Ernährungsbiologie der Larven von *Odagmia ornata* Meigen (Diptera: Simuliidae). 1. Die Filtriertätigkeit unter dem Einfluss von Fließgeschwindigkeit, Wassertemperatur und Futterkonzentration. *Archiv für Hydrobiologie/Suppl.* 59: 43–52.
- Schröder, P. 1980b. Zur Ernährungsbiologie der Larven von *Odagmia ornata* Meigen (Diptera: Simuliidae). 2. Morphometrische und physiologische Bezugsgrossen, Darmentleerung und -füllzeit, Ingestion. *Ibid.* 59: 53–95.
- Serra-Tosio, B. 1967. La prise de nourriture chez la larvae de *Prosimulium inflatum* Davies, 1957 (Diptera: Simuliidae). *Trav. Lab. Hydrobiol.* 57: 58: 97–103.
- Sioli, H. 1964. General features of the limnology of Amazônia. *Verh. Internationale Vereinigung für Limnologie* 15: 1053–1058.
- Wallace, J. B. and R. W. Merritt. 1980. Filter feeding ecology of aquatic insects. *Annual Review of Entomology* 25: 103–132.
- Whitton, B. A. 1975. Algae. pp 81–105 in B. A. Whitton (Ed.), *River Ecology*. University of California Press.
- Wotton, R. S. 1976. Evidence that blackfly larvae can feed on particles of colloidal size. *Nature (London)* 261: 697.
- Wotton, R. S. 1977. The size of particles ingested by moorland stream blackfly larvae (Simuliidae.) *Oikos* 29: 332–335.
- Wotton, R. S. 1978. The feeding-rate of *Metacnephia tredecimatum* larvae (Diptera: Simuliidae) in a Swedish lake outlet. *Ibid.* 32: 121–125.
- Wotton, R. S. 1979. The influence of a lake on the distribution of black-fly species (Diptera: Simuliidae) along a river. *Ibid.* 32: 368–372.
- Wotton, R. S. 1980a. Bacteria as food for blackfly larvae (Diptera: Simuliidae) in a lake-outlet in Finland. *Ann. Zool. Fennici* 17: 127–130.
- Wotton, R. S. 1980b. Coprophagy as an economic feeding tactic in blackfly larvae. *Oikos* 34: 282–286.



**TRENDS IN NUMBERS OF AQUATIC INVERTEBRATES IN A LARGE CANADIAN  
RIVER<sup>1</sup> DURING FOUR YEARS OF BLACK FLY LARVICIDING WITH  
METHOXYCHLOR (DIPTERA: SIMULIIDAE)**

*F. J. H. Fredeen*

*Agriculture Canada Research Station*

*107 Science Crescent*

*Saskatoon, Saskatchewan*

*S7N 0X2*

*Quaestiones Entomologicae*

*19: 53-92 1983*

**ABSTRACT**

*Methoxychlor was injected at about 0.3 parts a.i per million parts of water, maintained for 15 minutes, into the Saskatchewan River System in Saskatchewan once in 1976, six times in 1977, seven in 1978, 19 in 1979, and five times in 1980. Severe outbreaks of Simulium luggeri originated from various portions of the river up to 200 km long during the first three years, but not in 1979 or 1980.*

*With suprageneric taxa serving as units, trends in numbers of non-simuliids were measured 1977 through 1980. Average densities of combined non-simuliid invertebrate populations attaching weekly to artificial substrates in mid-river sites in all three branches of the Saskatchewan River peaked in 1979 ( $P < 0.01$ ) the year of maximum larvicide use, but in 1980 returned to just above the 1977 level. Average numbers of invertebrates in benthic samples from river margins also generally peaked in 1979 or 1980 in all three river branches. In one or more of the six locations sampled, however, numbers of certain families of Ephemeroptera (baetids, heptageniids, caenids, leptophlebiids, and polymitarcyids), of Trichoptera (hydroptilids, leptocerids, and brachycentrids), and of Diptera (simuliids, tanypodines, orthocladiines, tanytarsines, and empids) declined after 1977 or 1978; in other locations many of these taxa peaked in 1979 or 1980.*

*Some larvae dislodged by methoxychlor treatments apparently reattached in downstream sites. In 25 to 73 percent of 23 tests there were increases rather than decreases in numbers of various non-simuliid and simuliid taxa attaching to rope-piece substrates, 25 to 92 km downstream during the week following an injection.*

*In summary, significant upward trends in average annual densities of suprageneric taxa indicated that effects of methoxychlor treatments essentially were neutral when compared with effects of unidentified extrinsic ecological processes. Furthermore, check lists of benthic species collected from all three rivers at the conclusion of tests in 1980 proved the survival of a varied fauna representing apparently complete ranges in feeding habits, activity patterns and life cycles. Thus, the relatively intensive series of methoxychlor larvicide treatments required to prevent damaging outbreaks of *S. luggeri* from the Saskatchewan River was not permanently harmful to non-simuliid taxa in the river, at least at the suprageneric level.*

---

<sup>1</sup>The Saskatchewan River in Saskatchewan.

## RÉSUMÉ

Une solution de méthoxychlor (0.3 ppm d'ingrédients actifs) fut versée pendant 15 minutes dans le réseau de la rivière Saskatchewan à savoir: en 1976 (une fois), 1977 (six fois), 1978 (sept fois), 1979 (19 fois) et 1980 (cinq fois). Au cours des trois premières années, les populations de *Simulium luggeri* ont explosé à divers endroits de la rivière, atteignant une étendue de 200 km près.

En adoptant le niveau supragénérique comme critère de classification, l'auteur a dénombré les populations d'invertébrés non-simuliides de 1977 à 1980. La densité hebdomadaire moyenne de l'ensemble des populations s'attachant aux substrats artificiels placés au milieu du cours d'eau, dans la rivière Saskatchewan et ses deux tributaires, a culminé en 1979 ( $P < 0.01$ ), l'année d'utilisation maximale du larvicide. En 1980, cependant, la densité populations a diminué presque au niveau enregistré en 1977. Également, l'amplitude des moyennes d'invertébrés dans les échantillons prélevés du fond le long des rives a généralement culminé en 1979 ou en 1980 dans la rivière et ses deux tributaires. Toutefois, à l'un ou plusieurs des six sites échantillonnés, les populations de certaines familles d'Ephéméroptères, de Trichoptères et de Diptères ont diminué après 1977 ou 1978; aux autres sites, plusieurs de ces taxons ont culminé en 1979 ou 1980.

Des larves délogées par les traitements au méthoxychlor ont paru se réattacher plus bas dans la rivière. Dans 25 à 73% des 23 tests effectués, on a remarqué un accroissement inattendu du nombre des taxons simuliides et non-simuliides s'attachant à des substrats faits de corde, situés de 25 à 92 km en aval durant la semaine suivant l'application du larvicide.

En résumé, un accroissement annuel significatif de la densité moyenne des populations étudiées a indiqué un effet neutre des traitements. Les listes des espèces recouvrées de la rivière Saskatchewan et de ses deux tributaires en 1980 ont démontré la survie de toute une gamme d'organismes. L'auteur conclut que les traitements relativement intensifs nécessaires pour contrôler *S. luggeri* dans la rivière Saskatchewan n'ont pas affecté les taxons non-simuliides de façon permanente.

## TABLE OF CONTENTS

Introduction .....	54
Experimental .....	56
Results and Discussion .....	59
Need for Control of Black Flies at Sites of Breeding .....	89
Acknowledgements .....	91
References .....	91

## INTRODUCTION

Single 7.5- to 15-minute injections of methoxychlor [2,2-bis(p-methoxyphenyl)-1,1,1-trichloroethane] have been used to reduce populations of black fly larvae in selected sections of the Saskatchewan River in Saskatchewan almost every year, 1968 to the present time. Reports about efficacy and environmental impact of 12 injections during the first six years of these tests have been published (Fredeen, 1974, 1975).

In the final and most comprehensive test in that series, populations of aquatic insect larvae were measured weekly in one untreated site and in four treated sites spaced at 40 km intervals in the North Saskatchewan River, throughout 11 consecutive weeks commencing one week before a single 7.5 minute injection of 0.6 parts of methoxychlor per million parts of water (p.p.m.). Downstream 161 km from the injection point, 66 percent of larval instars three to six of *Simulium arcticum* Malloch and 96 percent of instars one and two disappeared within the first week. Larger percentages were removed from nearer sites. Larvae of plecopterans were similarly affected but ephemeropterans, trichopterans, and chironomids were less affected. All four treated sites were rapidly repopulated. Populations of chironomid larvae larger than one mm long equalled or exceeded pre-treatment densities within one to three weeks, ephemeropterans within one to four weeks, trichopterans in one to seven weeks, plecopterans in



four to five weeks, and simuliids within two to ten weeks. Populations of larvae smaller than one mm long were generally restored more rapidly. Fish were not visibly affected (Fredeen, 1975).

In 1979 this "single-injection" pattern for methoxychlor was registered in Canada for control of larvae of *S. arcticum* in large rivers. Before that, methoxychlor was registered for use in Canada as a black fly larvicide only if applied by air across networks of shallow streams in 200 m wide swaths centered 400 m apart. Dosages of about 25 to 85 g of active ingredient (a.i.) per swath - ha would have been achieved with this method, equivalent to less than 0.01 p.p.m., a.i. sustained for about 0.5 minutes in a deep river such as the Saskatchewan River. Such a dosage would not have been effective against black fly larvae in this river because tests showed that exposures to about 0.2 p.p.m., maintained for 15 minutes were only partly effective (Fredeen 1974). Furthermore, logistics and cost of applying aerial swaths at 400 m intervals throughout the entire infested portion of the Saskatchewan River (150 to 200 km) would have been impractical.

It is not surprising that certain large rivers are sources of troublesome, chronic outbreaks of insects. Nor is it surprising in view of wide differences in habitats between rivers, that varieties of troublesome species vary widely between rivers. Munroe (1951) and Peterson (1952) listed 34 species of Trichoptera, mainly hydropsychids, emerging in nuisance numbers from the Niagara River. Corbet *et al.* (1966) reported that eight species of Trichoptera, again mainly hydropsychids, dominated nuisance swarms of insects emerging from the St. Lawrence River at Montreal. These insects created allergic reactions among residents, and navigational problems for ships in the St. Lawrence Ship Channel and vehicles on nearby highways. Fremling (1960(a), (b)) reported that massive flights of two species of mayflies (*Hexagenia bilineata* (Say) and *H. limbata* (Serville)) and one species of caddisfly (*Cheumatopsyche campyla* Ross) caused major nuisance and health problems in cities along the upper Mississippi River. Fredeen (1969) reported that larvae of the black fly *S. arcticum* Malloch were widespread in rivers and streams draining the eastern slopes of the Rocky Mountains, and that massive outbreaks, resulting in livestock losses, originated from certain portions of the Saskatchewan and Athabasca Rivers. Thus of the five large Nearctic rivers reported to have produced troublesome numbers of aquatic insects, economically important outbreaks of black flies have originated only from the Saskatchewan and Athabasca Rivers.

In the early 1970's, *S. luggeri* Nicholson and Mickel replaced *S. arcticum* as the dominant black fly species breeding in the Saskatchewan River in Saskatchewan, and within a few years it became a major pest of man and non-hominid animals (Fredeen, 1977). These changes in black fly populations coincided with major changes in their larval environments in the Saskatchewan River system in the 1970's. Summertime monthly water-flow volumes declined in the South Saskatchewan River to as low as 7.5 percent of the long term monthly averages (June, 1977) and in the North Saskatchewan River to as low as 34 percent (August, 1975) (Environment Canada 1977, 1978, 1979, 1980, 1981). This occurred in part because of completion of three hydroelectric dams in the river system and in part because of widespread drought in the mid 1970's. Previously these rivers had been deep, swift and turbid during summer months. Now they are relatively shallow, slow-flowing and clear, allowing dense growths of several species of water weeds for the first time. These plants are favored attachment sites for larvae of *S. luggeri* and several other black fly species previously found only in smaller rivers. An increase in tolerance to methoxychlor is not considered to have been responsible for these changes of black fly species because populations of larvae in treated sections are continually replenished by downstream drift from extensive untreated sections of

the rivers. However, L.D. 50's for larvae of these species of black flies have not been determined.

These changes in black fly communities and river conditions forced changes in abatement strategies. Whereas *S. arcticum* required control only in May, *S. luggeri* cycles continuously throughout May to September. Thus, in some recent years, larvicide has been injected at two- to four-week intervals to prevent damaging outbreaks.

Furthermore, it became necessary to space larvicide injection sites closer together geographically. Vast beds of water weeds developed upon previously barren sand bars when the river became relatively shallow and clear due to the combined effects of drought and summertime impoundment of water behind newly-built hydroelectric dams (Fredeen, 1977). These weed beds not only provided large extensions of larval attachment sites but unfortunately also rendered larvicide treatments less effective, presumably because of filtering effects. Thus it is now sometimes necessary to space larvicide injection sites only 20 to 50 km apart to achieve adequate control.

A four-year environmental impact study reported herein was initiated in 1977 to investigate long-term effects of this recently intensified larviciding program. An earlier study (Fredeen 1975) had indicated that when a 161 km section of the North Saskatchewan River was treated with methoxychlor, populations of invertebrates were restored to pre-treatment densities within a few weeks.

## EXPERIMENTAL

### Larvicide

The larvicide used throughout was a commercial emulsifiable concentrate containing 0.24 kg methoxychlor per litre. Treatments were performed under federal and provincial permits, renewed annually.

### Injection sites

Locations of sites of larvicide injections are shown in Figure 1 and Table 1. All sites were located in central Saskatchewan within less than 130 km from the confluence of the north and south branches of the Saskatchewan River. Specific locations within each site that were used for injections and/or assessments are described in greater detail in the following pages.

Most injections were made from motorized ferries which allowed four continuous swaths across the entire river during each 15-minute injection. Only three injections were from fixed points instead of swaths across the river, all from a traffic bridge (Site 2, Fig. 1) spanning the North Saskatchewan River at Prince Albert in 1978. The main Saskatchewan River just downstream from the confluence of the north and south branches (Site 4) was injected from a Sikorsky helicopter with a long tube discharging just beneath the water surface. The helicopter crossed the river four times during each 15-minute injection.

Tests in 1977 and 1978 showed that injections from a single location (either Fenton Ferry Site 6 or Birch Hills Site 7) on the South Saskatchewan River were inadequate. Much of that river remained infested despite treatments, presumably because dense weed beds reduced effectiveness of the larvicide. Thus, in 1979 treatments sometimes were spaced 20 to 50 km apart and treatments also were initiated at the confluence (Site 4) when it became evident that treatments had not travelled effectively beyond that point.

TABLE 1. LIST OF SITES WHERE METHOXYCHLOR BLACK FLY LARVICIDE WAS INJECTED, AND/OR IMPACT STUDIES CONDUCTED, SASKATCHEWAN RIVER SYSTEM IN SASKATCHEWAN.

Site <sup>(1)</sup>	Distance to Confluence	
	(km)	(miles)
<i>North Saskatchewan River</i>		
1. Wingard Ferry	128	80
2. Prince Albert traffic bridge	61	38
3. Cecil Ferry	36	22
4. The Confluence, N. and S. Saskatchewan Rivers	0	0
<i>South Saskatchewan River</i>		
5. St. Laurent-Grandin Ferry	125	78
6. Fenton Ferry	73	45
7. Birch Hills Ferry	41	26
8. Weldon Ferry	20	12
4. The Confluence	0	0
<i>Main Saskatchewan River Below Confluence</i>		
4. The Confluence	0	0
9. Gronlid Ferry	71	44

<sup>(1)</sup>See Fig. 1 to locate these sites on map.

#### Sampling sites for invertebrate populations

Sampling sites were fixed throughout the four-year study period. Permanently untreated check sites were not selected at the outset because it was not possible to predict where larvicide would be injected in each of the four years and also because our research team was not large enough to cope with additional sites.

#### Sampling methods

Two methods were used consistently throughout the four summers to measure invertebrate populations: (a) artificial substrates (rope pieces) anchored in three mid-river locations to measure weekly increments of drifting populations; and (b) Surber-type net sampling in six locations along river margins to collect samples of benthic populations.

*Artificial substrates.*— One-m lengths of 0.5 cm diameter polypropylene rope (Fredeen and Spurr, 1978) served as artificial substrates. Each rope piece was anchored so that it floated just under the water surface. Polypropylene has the correct specific gravity for this purpose. Two anchors, each with one attached rope piece, were placed about mid-channel, about one km upriver from each of the three selected sites about one week after ice break-up each spring in water flowing at about 0.5 to 1.0 m/sec depending upon river volume. The rope pieces were collected and replaced with new rope pieces weekly throughout each summer. One pair of

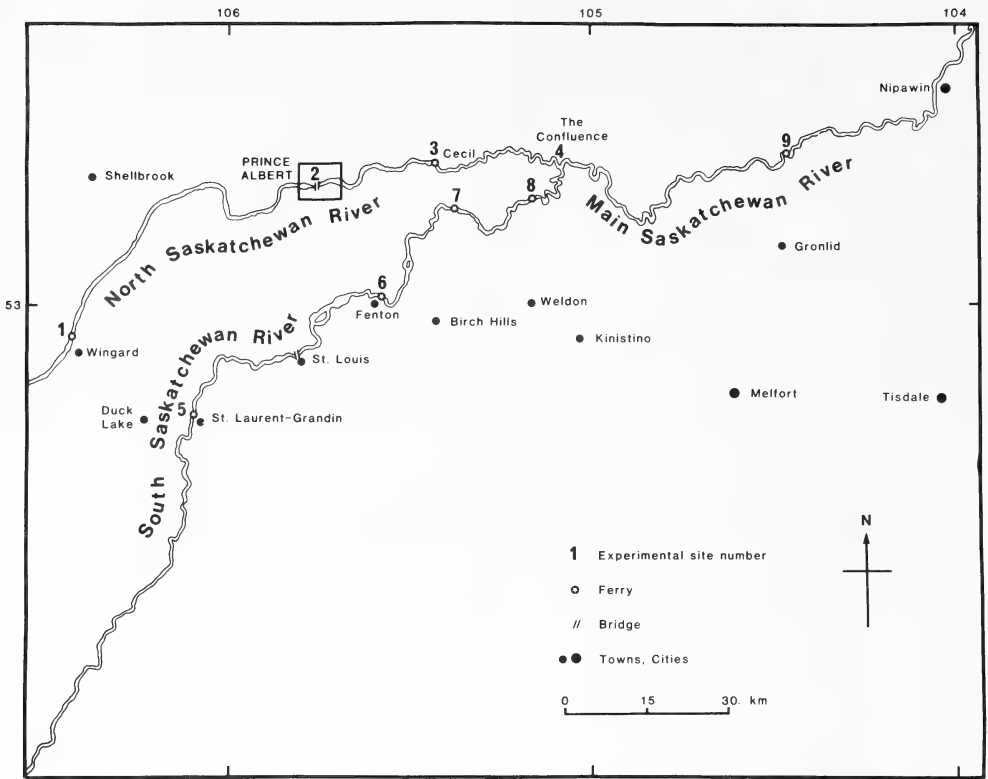


Fig. 1. Map showing experimental sites on the North, South, and Main Saskatchewan Rivers in Saskatchewan.

anchors was located about one km upstream from Cecil Ferry in the North Saskatchewan River (Site 3, Fig. 1), another pair was located about one km upstream from Birch Hills Ferry in the South Saskatchewan (Site 7), and the third pair was located about one km upstream from Gronlid Ferry in the main Saskatchewan River (Site 9). All three sites were served by "all weather" roads to ferries which ensured uninterrupted weekly access throughout all four summers. More than 60 percent of all larvicide injections occurred above these sites and 40 percent downstream (Tables 2, 3, and 4). Rope pieces were exchanged weekly for 17 consecutive weeks in Sites 3 and 7, and for 15 consecutive weeks in Site 9. The samples were individually preserved in 95 percent ethanol until analysis of attached invertebrates. Generally only one sample from each pair was analyzed.

These samples from artificial substrates were used for two purposes: (1) To provide weekly counts of immigrant populations of black fly larvae to estimate need for larvicide treatments. (A weekly accumulation of 1000 or more black fly larvae per 100 cm of rope indicated that larvae were arriving in numbers sufficient to cause damaging outbreaks unless controlled.); (2) To measure long-term trends in numbers of drifting invertebrates in mid-river locations. It was assumed that populations seen in these samples were related numerically to river bed populations from whence the drifting invertebrates had originated even though exact sources were not known (Fredeen and Spurr, 1978).

*Benthic samples.*— Samples of benthic invertebrates were collected from river margins under 50 to 60 cm of water with a 645 cm<sup>2</sup> Surber-type net with 0.2 mm mesh openings at

weekly intervals for three consecutive weeks each August. Rocky beds precluded sampling with an automatic dredge. The month of August was selected because larvicide treatments were completed by that time each year, and because river levels were generally stable or slowly declining, allowing weekly collections without interruptions, from permanently inhabited portions of the river bed accessible on foot. In 1979, a one-week interruption (August 21) of the weekly regime occurred due to a brief rise in the level of the South Saskatchewan River. In 1979, there were no collections from the main Saskatchewan River (Site 9) because of insufficient staff.

In each of the three selected weeks each year, five 645 cm<sup>2</sup> samples (from a total of approximately 3225 cm<sup>2</sup>) of river bed material to a depth of more than five cm were collected from each of six locations: each side of the North Saskatchewan River about one km above Cecil Ferry (Site 3), the north side of the North Saskatchewan about one km above the confluence (Site 4), the south side of the South Saskatchewan about two km above the confluence (Site 4), and each side of the main Saskatchewan River about one km above Gronlid Ferry (Site 9). Most sites were subjected to one or more larvicide treatments each year, the notable exception being the two Site 3 locations which were not treated in 1980. Collections from the North Saskatchewan River, Site 3 north side, were from the effluent path of a pulp mill, nine km upstream.

Each batch of five samples was combined into a single sample and preserved in 95 percent ethanol. Specimens were analyzed to families or sub-families. In 1980, keys became available for identification of species of Ephemeroptera, Plecoptera, Trichoptera, and Diptera inhabiting the Saskatchewan River in Saskatchewan, allowing preparation of a check list of species found in benthic samples during that year.

*Data analysis.*— Extreme variabilities characterized substrate and benthic populations ( $x_i$ ) and for analysis, logarithmic transformations of the form  $\log(x_i + 1)$  were applied. Transformed data were analyzed by the least squares method using the formula:  $y_{ij} = \mu + t_i + w_j + e_{ij}$  where  $y_{ij}$  was the transformed observation in the  $j^{\text{th}}$  week ( $w$ ) of the  $i^{\text{th}}$  year ( $t$ ). Anti-log conversions of least squares means obtained in analyses provided the average values shown in tables and text. All tests of significance were based upon transformed data.

## RESULTS AND DISCUSSION

### Physical and chemical condition of the rivers, 1977-1980

Ice-free conditions on the Saskatchewan Rivers commenced each year during the third week of April except in 1979 when it commenced May 3 for the north branch and May 12 for the south. Both rivers refroze during the second or third week of November each year.

Mean monthly water discharge rates for the North Saskatchewan River, 1977, 1978, 1979, and 1980 for the months of May, June, July, and August were about 365, 490, 410, and 260 m<sup>3</sup>/sec respectively, and for the south branch about 85, 165, 115, and 85 m<sup>3</sup>/sec for the same months (Environment Canada, 1978, 1979, 1980 and 1981; Fisheries and Environment Canada 1977).

Turbidity varied approximately with the discharge rates and ranged from about 10 to 1000 gm/m<sup>3</sup> of water in the north branch and from about 10 to 100 gm/m<sup>3</sup> in the south branch.

Mean daily water temperatures increased from about 1° to 22°C in May and ranged from 16° to 24°C in June, 17° to 27°C in July, and 14° to 23°C in August.

The pH ranged from about 7.9 to 9.0 in May to about 8.0 to 9.1 in August in both rivers.

Phenolphthalein alkalinity ranged from 0 to about 20 (as p.p.m.  $\text{CaCO}_3$ ) and total alkalinity ranged from about 100 to 200 (as p.p.m.  $\text{CaCO}_3$ ). Hardness ranged from about 130 to 200 p.p.m. (as  $\text{CaCO}_3$ ) in both rivers.

### Larvicide treatments

Complete lists of injections of methoxychlor into the north, south, and main branches of the Saskatchewan River, 1974 to 1980 inclusive, are shown in Tables 2, 3, and 4. All previous treatments were reported by Fredeen (1974, 1975).

The larviciding campaign on the Saskatchewan River System was expanded from one treatment in 1976 to six in 1977, seven in 1978, and 19 in 1979, in attempts to reduce intensity and duration of outbreaks of *S. luggeri* that frequently extended 100 to 150 km or even further from the river in 1976, 1977, and 1978. Initially, the campaign was based upon one developed for control of *S. arcticum*, where one or two larvicide injections per year were generally sufficient to prevent a major outbreak. However, *S. luggeri*, which became the dominant species in 1976, cycled continuously all summer, and larvae attached in large numbers in aquatic weed beds newly developed in shallow sections of the rivers. Injections spaced about four weeks apart in 1977 and 1978 successfully removed many larvae but the relatively long intervals between treatments allowed many other larvae to complete growth and produce abundant females which returned to re-populate the rivers with eggs. Also, injections from a single location in the South Saskatchewan River in 1977 and 1978 were inadequate. Much of that river sometimes remained infested, presumably because dense weed beds reduced effectiveness of the methoxychlor, perhaps by adsorbing it from the water. Furthermore, treatments did not seem to extend effectively beyond the confluence of the North and South Saskatchewan Rivers. Increasingly massive outbreaks originated from the main Saskatchewan River some 70 km or further downstream from the confluence in 1977 and 1978.

Requirement for increased numbers of methoxychlor treatments was believed not due to development of increased tolerance. Weekly samples collected from artificial substrates above Site 3 in 1980 and Site 7 in 1977, years in which these sites were not treated, showed that downriver drift of black fly larvae from untreated sections occurred continuously throughout each summer.

Thus in 1979, the program was expanded to allow as required (a) injections to be spaced closer together in time, (b) multiple simultaneous injections at several sites in the weedy South Saskatchewan River, and (c) injections for the first time into the main Saskatchewan River below the confluence. Infestations of larvae were treated with methoxychlor larvicide injected at eight locations that year, three of which were injected only once during the summer, two, twice, and the others, three to five times. Relatively few larvae were allowed to mature and produce adults. For the first time in four years, livestock and people along the entire river experienced major relief from black flies.

In 1980 only one injection was required on the North Saskatchewan River, two at two sites each on the south branch, and none on the main branch.

TABLE 2. COMPLETE LIST OF METHOXYCHLOR BLACK FLY LARVICIDE<sup>(1)</sup> TREATMENTS, NORTH SASKATCHEWAN RIVER, 1974 TO 1980, INCLUSIVE.

Year	Site <sup>(2)</sup>	Date	Volume discharge of river (M <sup>3</sup> /sec)	Amount of methoxychlor injected (kg. A.I.)	Av. conc. A.I. during 15-min injection (p.p.m.)
1974	No treatments	—	—	—	—
1975	3	May 27	286	80.4	0.312
1976	3	July 7	253	98.5	0.433
1977	3	May 19	337	85.8	0.283
1977	2	July 4	314	84.3	0.299
1977	3	August 2	248	62.5	0.280
1978	2	May 26	228	53.8	0.253
1978	2	June 20	583	135.0	0.257
1978	2	August 8	280	80.5	0.319
1979	1	June 5	360	102.0	0.315
1979	1	June 21	235	58.6	0.278
1979	1	July 17	242	53.9	0.248
1979	1	July 31	273	59.4	0.242
1979	1	August 16	214	53.9	0.280
1979	3	August 1	239	64.8	0.302
1980	3	May 16	198	70.0	0.391

<sup>(1)</sup>Emulsifiable concentrate containing 0.24 kg active ingredient per litre.

<sup>(2)</sup>See Fig. 1 to locate sites on map, and Table 1 for distances.;

TABLE 3. COMPLETE LIST OF METHOXYCHLOR BLACK FLY LARVICIDE<sup>(1)</sup>  
TREATMENTS, SOUTH SASKATCHEWAN RIVER, 1974 TO 1980, INCLUSIVE.

Year	Site <sup>(2)</sup>	Date	Volume discharge of river (M <sup>3</sup> /sec)	Amount of methoxychlor injected (kg. A.I.)	Av. conc. A.I. during 15-min injection (p.p.m.)
1974	No treatments	—	—	—	—
1975	No treatments	—	—	—	—
1976	No treatments	—	—	—	—
1977	7	May 19	66	10.6	0.177
1977	7	July 4	53	13.2	0.277
1977	7	August 2	55	12.6	0.253
1978	6	May 26	56	10.9	0.211
1978	6	June 20	430	107.7	0.278
1978	6	July 21	217	59.3	0.304
1978	6	August 8	175	80.5	0.510
1979	5	June 5	274	80.5	0.327
1979	5	June 21	130	43.0	0.368
1979	5	July 12	72	16.3	0.251
1979	6	June 28	81	27.2	0.373
1979	6	July 12	72	16.3	0.251
1979	7	June 28	81	27.2	0.373
1979	7	July 12	72	16.3	0.251
1979	8	July 12	72	16.3	0.251
1980	6	May 16	86	27.0	0.349
1980	6	June 11	56	10.9	0.216
1980	7	May 16	86	27.0	0.349
1980	7	June 11	56	10.9	0.216

<sup>(1)</sup>Emulsifiable concentrate containing 0.24 kg active ingredient per litre.

<sup>(2)</sup>See Fig. 1 to locate sites on map, and Table 1 for distances.



TABLE 4. COMPLETE LIST OF METHOXYCHLOR BLACK FLY LARVICIDE<sup>(1)</sup>  
TREATMENTS, MAIN SASKATCHEWAN RIVER, 1974 TO 1980, INCLUSIVE.

Year	Site <sup>(2)</sup>	Date	Volume discharge of river (M <sup>3</sup> /sec)	Amount of methoxychlor injected (kg. A.I.)	Av. conc. A.I. during 15-min injection (p.p.m.)
1974	No treatments	—	—	—	—
1975	No treatments	—	—	—	—
1976	No treatments	—	—	—	—
1977	No treatments	—	—	—	—
1978	No treatments	—	—	—	—
1979	4	June 6	625	177.0	0.318
1979	4	June 22	370	113.0	0.295
1979	4	July 13	340	86.0	0.281
1979	4	August 16	280	70.2	0.279
1979	9	August 1	332	81.2	0.273
1980	No treatments	—	—	—	—

<sup>(1)</sup>Emulsifiable concentrate containing 0.24 kg active ingredient per litre.

<sup>(2)</sup>See Fig. 1 to locate sites on map, and Table 1 for distances.

## Benthos, River Margins      Substrates, Mid-River

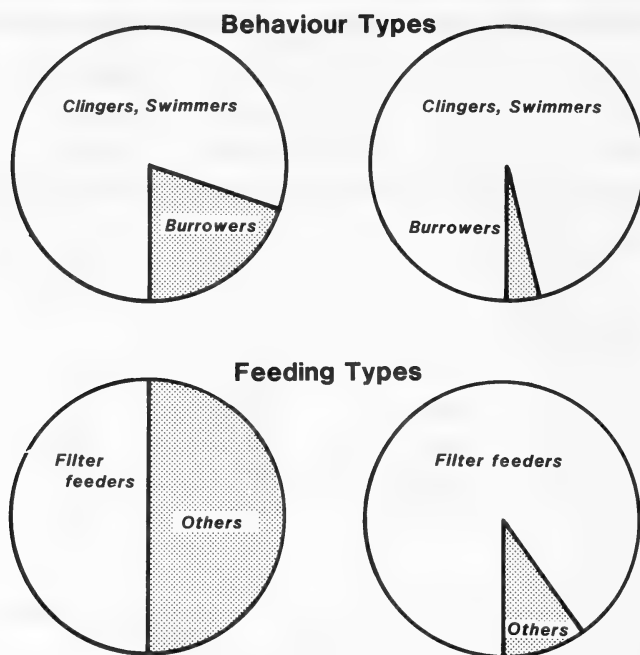


Fig. 2. Diagrammatic representations of approximate proportions of invertebrates representing major behaviour and feeding types in marginal benthos and in mid-river substrate samples collected from the Saskatchewan River, 1977 through 1980.

### Habits and trophic relationships of invertebrates collected

*Insect larvae.*— The varied habits and trophic relationships of larvae of aquatic insects inhabiting the Saskatchewan River (Table 5, Fig. 2) are important when considering potential impact of larvicide treatments. In benthos samples from the margins of the Saskatchewan River most taxa (representing about 80 percent of the total insects collected) were considered to be clingers or climbers (Merritt and Cummins, 1978). The remainder, mainly *Chironomus* spp. and tanytarsines, as well as the rarer polymitarcyids and anisopterans were presumed to be burrowers or tube builders. The relatively abundant hydropsychids inhabited fixed retreats. About one percent of the total population were case-building trichopterans.

In samples from artificial substrates from mid-river sites more than 95 percent of the total insects collected were clingers or climbers.

Regarding feeding habits, according to Cummins (1973), Merritt and Cummins (1978), and Wiggins (1977), most or all of our ephemeropterans, trichopterans, and dipterans were considered to be collectors of periphyton, debris, and plankton. Many of these, including simuliids, hydropsychids, and many species of Ephemeroptera, Chironomini, and Tanytarsini, were filter feeders. In benthos samples about 50 percent of the larvae were considered to be filter feeders (Fig. 2) and in samples from mid-river artificial substrates about 90 percent (mainly simuliids) were filter feeders. About two-thirds of the remainders were assumed to

TABLE 5. HABITS AND TROPHIC RELATIONSHIPS<sup>(1)</sup> OF AQUATIC INSECTS INHABITING THE SASKATCHEWAN RIVER IN SASKATCHEWAN.

Taxa	Habits	Trophic Relationships
<b>EPHEMEROPTERA</b>		
Siphonuridae: <i>Isonychia</i>	Swimmers, clingers	Collectors (filterers); engulfers (predators)
Baetidae: <i>Baetis</i>	Swimmers, climbers, clingers	Collectors (gatherers) (detritus, diatoms); scrapers
<i>Pseudocloeon</i>	Swimmers, clingers	Scrapers; collectors (gatherers)
Heptageniidae: <i>Heptagenia</i>	Clingers, swimmers	Scrapers; collectors (gatherers) (engulfers)
<i>Stenonema</i>	Clingers	Collectors (gatherers); scrapers
Ephemerellidae: <i>Ephemerella</i>	Clingers, swimmers	Collectors (gatherers) (detritus, algae)
Tricorythidae: <i>Tricorythodes</i>	Sprawlers, clingers	Collectors (gatherers)
Caenidae: <i>Caenis</i>	Sprawlers	Collectors (gatherers); scrapers
Leptophlebiidae: <i>Traverella</i>	Clingers	Collectors (filterers)
Polymitarcyidae: <i>Ephoron</i>	Burrowers	Collectors (gatherers)
<b>ODONATA</b>		
Anisoptera: <i>Ophiogomphus</i>	Burrowers	Engulfers (predators)
Zygoptera: <i>Ischnura</i>	Climbers	Engulfers (predators)
<b>PLECOPTERA</b>		
Pteronarcidae: <i>Pteronarcys</i>	Clingers, sprawlers	Shredders (detritivores) engulfers (predators)
Perlidae: <i>Acroneuria</i>	Clingers	Engulfers (predators)
HEMIPTERA: <i>Sigara</i>	Swimmers, climbers	Piercers (herbivores); collectors (gatherers)
<b>COLEOPTERA:</b>		
Dytiscidae: <i>Deronectes</i>	Swimmers, climbers	Piercers (carnivores)
Helodidae	Climbers	Scrapers; collectors; shredders; piercers (herbivores)
<b>TRICHOPTERA</b>		
Psychomyiidae: <i>Psychomyia</i>	Clingers (tube retreats)	Collectors (gatherers)
Polycentropodidae: <i>Neureclipsis</i>	Clingers (net builders)	Collectors (filterers) (herbivores, predators)

(continued on next page)

Table 5 (continued)

Taxa	Habits	Trophic Relationships
Hydropsychidae:		
<i>Cheumatopsyche</i>	Clingers (net builders)	Collectors (filterers) (herbivores, predators)
<i>Hydropsyche</i>	Clingers (net builders)	Collectors (filterers) (herbivores, predators)
Hydroptilidae: <i>Hydroptila</i>	Clingers (case builders)	Piercers; scrapers (herbivores)
<i>Maytrichia</i>	Clingers (case builders)	Piercers; scrapers (herbivores)
Brachycentridae:		
<i>Brachycentrus</i>	Clingers (case builders)	Collectors; filterers; scrapers (herbivores, predators)
Leptoceridae: <i>Ceraclea</i>	Sprawlers, climbers (case builders)	Collectors; shredders (herbivores, predators)
<i>Nectopsyche</i>	Climbers (case builders)	Shredders; collectors (herbivores, predators)
<i>Oecetis</i>	Clingers, climbers (case builders)	Engulfers, shredders (predators, herbivores)

collect food by 'gathering' rather than by 'filtering' and about one third were assumed to be either herbivores (piercers or shredders) or carnivores (Table 5).

In general, the invertebrate fauna of the Saskatchewan River was dominated by filter-feeding black fly larvae (tables 6, 7, 8, 9).

*Crustaceans*.— Five major taxa of crustaceans were collected. All could be considered free-swimming although in these rivers they would have lived near or on the substratum (Ward and Whipple 1959). Ostracods comprised about 80 percent of the total crustacean population and occurred regularly in all six sites sampled with the Surber-type net. Copepods and cladocerans were found in the North and South Saskatchewan Rivers but not in the main river below the confluence. Conchostracans and malacostracans were seldom collected.

Ostracods and copepods are shredders and feed on decaying plant and animal materials. Cladocerans are filterers (plankton) and malacostracans (*Hyalella* spp.) are shredders and filterers.

*Acari*.— Larvae of Parasitengona, found in all sites, are parasitic on aquatic insects and the adults are predaceous.

*Mollusca*.— Pelecypods (Sphaeriidae) were relatively abundant and widely distributed in the Saskatchewan River. They are filterers, subsisting on detritus and plankton. Gastropods (mainly Ancyliidae) were scarcer and less widely distributed. They are browsers, feeding on algae and detritus.

### Identification of Invertebrates

It was within our expertise to identify Simuliidae to species from the outset. However, keys to identify many species in other major taxa were not available until after we had completed analyzing substrate and benthic samples in 1980. All samples have been retained at our Research Station in the event that identification of additional taxa to species levels would eventually prove productive.

### Trends in numbers of invertebrates attached to artificial substrates

Population trends for taxa sampled with artificial substrates weekly during the summers of 1977 to 1980, inclusive, are given for the North Saskatchewan River (Site 3) in Table 6, for the South Saskatchewan River (Site 7) in Table 7, and for the main Saskatchewan River about 70 km downriver from the confluence of the two branches (Site 9) in Table 8.

Note that Site 3 received only one treatment in 1977, three in 1978, five in 1979 and none in 1980. Site 7 received no treatments in 1977, four in 1978, five in 1979 and two in 1980. The main Saskatchewan River below the confluence was not treated in 1977, 1978 or 1980 so that Site 9 received four treatments in 1979 but none in the other three years unless one assumes that effects from some or all of the six, seven, 14, and five injections into the two branches above the confluence may have affected populations at Site 9. Permanently untreated check sites were not available for reasons stated earlier in this paper.

Mites peaked in 1979 at Sites 3 and 7 ( $P < 0.01$  at Site 7) and in 1980 at Site 9 ( $P < 0.01$ ). This suggests that there were parallel increases in numbers of certain invertebrate taxa upon which these animals preyed. Alternatively, as discussed in a following section, displaced larvae may have reattached further downriver.

Mean annual numbers of plecopterans attaching weekly to artificial substrates declined after 1978 at Site 3 ( $P < 0.01$ ) but remained relatively unchanged at Sites 7 and 9. Larvae of ephemeropterans remained relatively abundant and unchanged in numbers at Sites 3 and 7 but peaked in 1980 at Site 9 ( $P < 0.01$ ). Larvae of trichopterans remained relatively abundant but unchanged in numbers at all three sites. Larvae of chironomids, the most abundant of all non-simuliid taxa, peaked in 1979 in all three sites with highly significant differences between years in Sites 7 and 9 ( $P < 0.01$ ).

Numbers of larvae of *S. luggeri* declined annually after 1977 in Site 3 (n.s.) and after 1978 in Sites 7 and 9 ( $P < 0.01$  at both sites) to four-year lows in all three sites. Numbers of *S. arcticum* and *S. meridionale* Riley were relatively small compared to numbers of *S. luggeri* and remained unchanged in Sites 3 and 9, but declined after 1977 in Site 7 ( $P < 0.05$ ). Numbers of *S. vittatum* Zetterstedt peaked in 1977 in Site 7 ( $P < 0.01$ ) and in 1979 in Site 9 ( $P < 0.01$ ).

Larvae of these four species of *Simulium* were considered to be relatively susceptible to methoxychlor, not only because they inhabited sites that would have ensured direct contact with the larvicide but also because they were filter feeders and thus would have ingested suspended particles containing adsorbed methoxychlor (Fredeen *et al.*, 1975). Despite this, no single species of *Simulium* was eliminated during the four years of treatment. In fact, *S. vittatum* (not a pest species) actually attained maximum abundance at two sites in 1979, the year of maximum use of methoxychlor.

These data help to explain why prominent non-simuliid taxa remained abundant, and of greater importance, suggest that trends in numbers of each non-simuliid order or family as shown in Tables 6, 7, 8 and 9 are actually representative of parallel trends in numbers of most or all of the species comprising those suprageneric taxa.

Densities of populations of invertebrates on rope-piece substrates were believed related to densities of the benthic populations from whence the drifting populations had originated. Substrates offered convenient means of obtaining uninterrupted series of weekly samples from otherwise inaccessible mid-river sites throughout the four-year study. However, it was not possible to determine how far larvae had drifted in the rivers before attaching to the substrates. Presumably many (most?) larvae originated from treated sections of the rivers because

TABLE 6. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES ATTACHED TO ROPE PIECES<sup>(2)</sup> ANCHORED FOR ONE-WEEK PERIODS THROUGHOUT 17 WEEKS EACH YEAR, MAY TO SEPTEMBER, ONE KM UPRIVER FROM SITE 3<sup>(3)</sup> (CECIL FERRY), NORTH SASKATCHEWAN RIVER, SASKATCHEWAN, 1977 TO 1980 INCLUSIVE.

Year	1977	1978	1979	1980	All years combined	Significance of differences between years <sup>(4)</sup>
Number of larvicide injections above this site	1	3	5	0		
ACARI	0.14a	0.18a	1.11b	0.34ab	0.40	n.s.
PLECOPTERA	0.68ab	3.75c	1.56bc	0.21a	1.21	P<0.01
EPHEMEROPTERA	27.15a	20.13a	45.59a	54.04a	34.14	n.s.
TRICHOPTERA	28.41a	25.63a	25.41a	31.19a	27.56	n.s.
Chironomidae	192.64a	170.40a	622.73b	135.46a	229.67	n.s.
<i>S. luggeri</i>	3236.43b	2439.05b	1855.26ab	921.36a	1916.79	n.s.
<i>S. arcticum</i>	18.58a	17.75a	21.73a	21.90a	19.91	n.s.
<i>S. meridionale</i>	28.60a	41.48a	31.29a	61.88a	38.98	n.s.
<i>S. venustum</i> etc.	0.00a	0.23ab	1.03b	0.00a	0.26	P<0.05
<i>S. vittatum</i>	215.52ab	95.72a	1175.25b	65.42a	200.09	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>Polypropylene rope: length = 100 cm; diam. = 0.5 cm.

<sup>(3)</sup>See Fig. 1 to locate sites on map, and Table 1 for distances.

<sup>(4)</sup>These statistics were calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly ( $P < 0.05$ ) as indicated by Duncan's New Multiple Range tests.

TABLE 7. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES ATTACHED TO ROPE PIECES<sup>(2)</sup> ANCHORED FOR ONE-WEEK PERIODS THROUGHOUT 17 WEEKS EACH YEAR, MAY TO SEPTEMBER, ONE KM UPRIVER FROM SITE 7<sup>(3)</sup> (BIRCH HILLS FERRY), SOUTH SASKATCHEWAN RIVER, SASKATCHEWAN, 1977 TO 1980 INCLUSIVE

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(4)</sup>
Number of larvicide injections above this site	0	4	5	2		
ACARI	0.10a	1.18a	17.69c	5.50b	3.13	P<0.01
PLECOPTERA	1.16b	0.58ab	0.87a	0.10a	0.63	n.s.
EPHEMEROPTERA	29.23a	15.33a	23.65a	23.55a	22.38	n.s.
TRICHOPTERA	41.42a	33.90a	42.90a	28.11a	36.09	n.s.
Chironomidae	72.86ab	104.08b	143.05b	41.84a	82.18	P<0.01
<i>S. luggeri</i>	1045.41b	1550.67b	270.83a	229.45a	563.68	P<0.01
<i>S. arcticum</i>	7.10b	6.02b	2.14ab	1.12a	3.41	P<0.05
<i>S. meridionale</i>	0.72b	0.00a	0.22ab	0.17a	0.25	P<0.05
<i>S. venustum</i> etc.	0.04a	0.22a	3.76b	0.14a	0.62	P<0.01
<i>S. vittatum</i>	246.46c	82.43b	21.52a	33.21ab	62.15	P<0.01

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>Polypropylene rope: length = 100 cm; diam. = 0.5 cm.

<sup>(3)</sup>See Fig. 1 to locate sites on map, and Table 1 for distances.

<sup>(4)</sup>These statistics were calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly ( $P < 0.05$ ) as indicated by Duncan's New Multiple Range tests.

TABLE 8. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES ATTACHED TO ROPE PIECES<sup>(2)</sup> ANCHORED FOR ONE-WEEK PERIODS THROUGHOUT 15 WEEKS EACH YEAR, MAY TO SEPTEMBER, ONE KM UPRIVER FROM SITE 9<sup>(3)</sup> (GRONLID FERRY), MAIN SASKATCHEWAN RIVER, SASKATCHEWAN, 1977 TO 1980 INCLUSIVE

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(5)</sup>
Number of larvicide injections above this site <sup>(4)</sup>	0 (6)	0 (7)	4 (18)	0 (5)		
ACARI	0.05a	0.54ab	1.30bc	3.04c	0.97	P<0.01
PLECOPTERA	0.16a	0.11a	0.23a	0.28a	0.19	n.s.
EPHEMEROPTERA	10.48a	5.51a	9.15a	39.23b	12.22	P<0.01
TRICHOPTERA	11.53a	30.46a	16.16a	23.22a	19.12	n.s.
Chironomidae	38.44a	54.72ab	115.04b	24.95a	49.72	P<0.01
<i>S. luggeri</i>	158.11ab	603.51c	315.23bc	61.55a	207.83	P<0.01
<i>S. arcticum</i>	3.23a	6.30a	6.99a	4.50a	5.07	n.s.
<i>S. meridionale</i>	0.72a	0.20a	0.67a	0.13a	0.40	n.s.
<i>S. venustum</i> etc.	0.00a	0.00a	2.16b	0.00a	0.33	P<0.01
<i>S. vittatum</i>	52.83b	2.71a	191.35b	4.10a	20.04	P<0.01

(1)Geometric means calculated from  $\log_{10}(x + 1)$  values.

(2)Polypropylene rope: length = 100 cm; diam. = 0.5 cm.

(3)See Fig. 1 to locate sites on map, and Table 1 for distances.

(4)Numbers in brackets indicate numbers of treatments in the entire Saskatchewan River system above the sampling site. Unbracketed numbers indicate numbers of treatments in the Main Saskatchewan River alone.

(5)These statistics were calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly ( $P < 0.05$ ) as indicated by Duncan's New Multiple Range tests.



TABLE 9. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES ATTACHED TO ROPE PIECES<sup>(2)</sup> ANCHORED FOR ONE-WEEK PERIODS THROUGHOUT 15 WEEKS EACH YEAR, MAY TO SEPTEMBER, 1977 TO 1980 INCLUSIVE. COMBINED DATA FROM THREE SITES<sup>(3)</sup>, SASKATCHEWAN RIVER, SASKATCHEWAN.

	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(4)</sup>
Total non-simuliids	162.68a	201.30a	423.62b	167.27a	219.29	P<0.01
Total Simuliidae except <i>S. vittatum</i>	982.78b	1540.35b	627.35ab	321.40a	743.39	P<0.01
Total Simuliidae including <i>S. vittatum</i>	1488.36b	1765.04b	1882.65b	408.26a	1015.25	P<0.01

<sup>(1)</sup>Geometric means calculated from  $\log_{10} (x + 1)$  values.

<sup>(2)</sup>Polypropylene rope: length = 100 cm; diam. = 0.5 cm.

<sup>(3)</sup>One km upriver from each of sites 3, 7, and 9 (Fig. 1), in the North, South, and Main Saskatchewan Rivers respectively.

<sup>(4)</sup>These statistics were calculated from  $\log_{10} (x + 1)$  values. Means followed by different letters, differ significantly ( $P < 0.05$ ) as indicated by Duncan's New Multiple Range tests.

TABLE 10. PERCENTAGES OF METHOXYCHLOR LARVICIDE TESTS IN WHICH SAMPLES OF AQUATIC INVERTEBRATES FROM ROPE-PIECE SUBSTRATES<sup>(1)</sup> WERE LARGER THAN THOSE OF THE PREVIOUS WEEK, SASKATCHEWAN RIVER SYSTEM, 1977 TO 1980, INCLUSIVE.

Larvicide injection 7 to 14 days earlier	Yes	Yes	No
Distance upstream from substrates (km)	71-92	25-32	
Number of tests <sup>(2)</sup>	11	12	36
Percentages of tests showing increased densities (%)			
ACARI	64	38	25
PLECOPTERA	37	25	28
EPHEMEROPTERA	64	33	61
TRICHOPTERA	64	58	61
Chironomidae	73	50	56
Simuliidae	64	33	36

<sup>(1)</sup>One-metre lengths of 0.5 cm diameter polypropylene rope anchored for one week at sites 3, 7, and 9 (Fig. 1).

<sup>(2)</sup>Data from many weeks during the four summers could not be included because:

- a.) the river was reinjected within less than two weeks before post-treatment samples could be collected,
- b.) injections were repeated on one date in more than one site in a single river,
- c.) samples from site 9 in the Main Saskatchewan River were not included in this summation if either of the two branches above the confluence had been injected within the two previous weeks.

sampling sites were located many km downriver from many or all larvicide injection sites. The most distant injection sites upstream from the three sampling sites were 92 km for Site 3, 84 km for Site 7 and 198 km for Site 9.

In summary, combined data from numbers of invertebrates attaching weekly to artificial substrates anchored mid-river in three sites (Table 9) show that mean densities of non-simuliid taxa in treated sections of these rivers peaked in 1979, but in 1980 returned to about 1977 densities. Differences between years were highly significant ( $P < 0.01$ ). Mean annual densities of simuliids (excluding *S. vittatum*) peaked in 1978 and then declined rapidly during the final two years of the program to a four-year low in 1980 (about one-fifth the density of 1978) and differences between years were highly significant. When numbers of *S. vittatum* larvae are included in these means, total populations peaked in 1979 and then also declined in 1980 to about one-fifth of the peak value. *S. vittatum* larvae were totalled separately because some females of this species laid eggs on floats supporting rope-piece substrates and some larvae found attached to the rope pieces may have hatched from those eggs rather than arriving as drifting larvae.

#### **Increases in numbers of invertebrates following larvicide injections**

Many collections of invertebrates from mid-river rope-piece substrates were larger immediately after larvicide injections than before (Table 10). This was particularly true for rope pieces anchored at relatively great distances downstream from injection sites. Thus collections from rope pieces anchored for one week 71 to 92 km downstream from an injection site contained larger numbers of mites, ephemeropterans, trichopterans, chironomids, and simuliids in 64 to 73 percent of the samples collected immediately after an injection than before. In 37 percent of those same post-treatment collections, numbers of plecopterans were larger than in pre-treatment collections.

From substrates anchored nearer the injection sites (i.e. 25 to 32 km downstream) numbers of these same taxa in post-treatment samples exceeded those in pre-treatment collections in only 25 to 58 percent of the collections.

In comparison, in the absence of larvicide treatments, consecutive weekly pairs of collections showed increases in the second week in 36 to 61 percent of the samples (Table 10).

These data provided new evidence that certain detached larvae survived and successfully reattached in sites further downriver as reported earlier by Fredeen (1974, 1975). The relatively substantial recolonization following methoxychlor treatments would also have been aided by regular drift of larvae newly hatched from eggs unaffected by methoxychlor, and larvae from untreated upstream sections and from protected niches in treated sections. Fredeen (1975) showed that larvae in sand beds in the Saskatchewan River were entirely unaffected by passage of methoxychlor-treated water. Pupae in general appeared to be resistant to methoxychlor and as well, pupae of certain chironomids and hydroptilids drifted into treated sections, attached to fragments of water weeds.

A prerequisite to successful reattachment by larvae would have been the reduction of methoxychlor concentrations to tolerable levels. The main Saskatchewan River downstream from the confluence would generally have received diluted larvicide from the branches. Although both branches above the confluence often were injected with methoxychlor on the same day (Tables 2 and 3) it was very unlikely that treated masses of water arrived at the same time at the confluence.

Also Fredeen *et al.* (1975) showed that as an injected mass of water travelled downstream it became progressively attenuated due to friction with the river bed. Furthermore adsorption to river bed sand was demonstrated. Alternatively, adsorption of methoxychlor to particles suspended in the water, especially in the relatively turbid North Saskatchewan River, would have aided long distance transport of methoxychlor.

Adsorption to water weeds, and filamentous algae, especially in extensive beds of several species in the South Saskatchewan River, was not proved but may be assumed. Edwards and Glass (1971), Butler *et al.* (1975), Paris and Lewis (1976) and others demonstrated that methoxychlor was rapidly adsorbed to grass, many species of algae, fungi and bacteria.

Data from limited laboratory tests indicate that larvae of certain aquatic invertebrates are less susceptible to methoxychlor than are black fly larvae. Sebastien and Lockhart (1981) showed that 100 percent of stonefly nymphs (*Pteronarcys dorsata* Say) were moribund after 24 hours of exposure to 0.3 mg/l of methoxychlor formulated as an emulsifiable concentrate, in recirculated, dechlorinated water at 17°C. Forty-eight hours of exposure of chironomid larvae (*Chironomus tentans* Fabricius) to 0.3 mg/l at 20°C followed by 48 hours in fresh water produced 99 percent mortality. In comparison, fifth and sixth instar black fly larvae (*S. decorum* Walker) suffered 100 percent detachment during 16-minute exposure to 0.3 mg/l of methoxychlor at 19°C, and 100 percent mortality when returned to fresh water for about 20 hours. Fredeen (1972) reported that the L.C. 50 for relatively full-grown larvae of *Hydropsyche morosa* Hagen following a six-hour exposure at 10°C to methoxychlor and 18 hours in fresh water was 0.04 mg/l of methoxychlor. Anderson and DeFoe (1980) reported that following continuous exposure to methoxychlor in flowing water throughout 28 days the L.C. 50 for the isopod *Asellus communis* Say was 0.42 µg/l, and for *Hydropsyche* sp. larvae was 1.3 µg/l. Stonefly larvae *P. dorsata* Say and a snail *Physa integra* did not die at the highest concentration tested, 4.2 µg/l.

Muirhead-Thomson (1973) suggests several reasons why one cannot use data from laboratory bioassays of toxicants to accurately predict events in field tests. Furthermore, the above bioassays were based upon relatively long exposures (6 hours to 28 days) whereas in our field tests with methoxychlor a treated pulse of water lasted only 15 minutes at the point of origin. Nevertheless, data quoted above from these few bioassays, and especially those from Sebastien and Lockhart (1981) suggest that certain non-simuliid species are less sensitive than simuliid larvae to small concentrations of methoxychlor.

### **Long-term effects of downstream displacements of larvae**

As to long-term effects of downstream displacements of larvae due to larvicide injections and other causes, comparisons of data presented in Tables 6, 7, and 8 show that numbers of mites, plecopterans and ephemeropterans attaching weekly to artificial substrates anchored in Site 9 (about 70 km below the confluence) peaked in 1980, one to three years after peaks were observed in the tributaries (Sites 3 and 7). Numbers of trichopterans did not trend significantly at any of the three sites but remained relatively abundant throughout the four years. Larvae of chironomids also remained abundant throughout but peaked in all three sites in the same year (1979) and differences between years were highly significant. Identification to the species level may have revealed differences in responses between species in each of these major taxa but this was not investigated. For reasons previously explained, changes in species complexes are believed not to have occurred.

Downstream displacements of black fly larvae presumably were responsible for increasingly dense accumulations of larvae of *S. luggeri* in the main Saskatchewan River and in the downstream end of the South Saskatchewan which resulted in major outbreaks from those regions in 1977 and 1978. Average weekly numbers of larvae of *S. luggeri* near Site 7, South Saskatchewan River (Table 7) increased from 1045 in 1977 (the year that that river was injected below the collecting site) to 1551 in 1978 when the river was injected some 32 km upstream (Tables 1 and 3). But when this weedy river was injected at four sites in 1979, average number of larvae was reduced to 271 per week and there were no destructive outbreaks that year from the South Saskatchewan River.

In the North Saskatchewan River treatments carried longer distances, presumably because that river was deeper, more turbid, and contained sparser weed beds. Injections at single sites (Table 2) were sufficient to steadily reduce populations of black fly larvae from a weekly mean of 3236 larvae in 1977 to 921 in 1980 (Table 6).

In the main Saskatchewan River at Site 9, mean weekly populations of black fly larvae attaching to artificial substrates increased from 158 in 1977 to 604 in 1978 (Table 8) apparently due to downstream drift of larvae from the North and South Saskatchewan Rivers. There were numerous severe outbreaks along the entire main Saskatchewan River in 1978. Some outbreaks inflicted losses 100 or more km from the river. Outbreaks were reduced to tolerable levels in 1979 following initiation of methoxychlor treatments that year at the confluence (Table 4).

### Trends in numbers of invertebrates in benthic samples

Quantitative samples of benthic organisms collected with Surber-type nets each August provided additional substantial evidence of increases in populations of many taxa and of non-significant trends in others between 1977 and 1979 or 1977 and 1980 (Tables 11 to 17). Details of living habits and trophic relationships are shown in Table 5.

Populations of crustaceans in four of the six locations (all three rivers) attained peak abundance in either 1979 or 1980 ( $P < 0.01$  in three sites). In only one location (Site 3, north side, in the effluent path of a pulp mill located nine km upstream from the sampling site) did crustaceans decline in abundance after 1977 ( $P < 0.05$ ). Ostracods comprised about 80 percent of the total populations; copepods and cladocerans about 20 percent. Conchostracans and malacostracans (*Hyalella* sp.) were rare throughout. All could be considered free-swimming although in lotic waters they would have lived on or in the substratum which may have offered them some protection from passage of the treated masses of water.

Mean August numbers of larvae of all taxa of Ephemeroptera combined, peaked in all six locations in 1980. Differences between years were significant in all three locations in the North Saskatchewan River, highly significant in the South Saskatchewan, but not significant in the main Saskatchewan River.

Examining data for various families of Ephemeroptera individually, baetids (about 98 percent *Baetis* nr. *pluto*) were relatively abundant and peaked in 1980 in at least one location in each of the three river branches. Differences in means between years were significant only in the South Saskatchewan River. Heptageniids (about 80 percent *Heptagenia* spp.), also relatively abundant in most locations, peaked in 1979 in the North Saskatchewan River (Site 3, south side) with significant differences between years in Site 3, north side in 1980 and the North Saskatchewan near the confluence in 1978. In the South Saskatchewan near the confluence they peaked in 1979, and in the main Saskatchewan River (Site 9) in 1977 (no

TABLE 11. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED ABOUT ONE KM UPRIVER FROM SITE 3 (CECIL FERRY), NORTH SASKATCHEWAN RIVER, SOUTH SIDE.

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(3)</sup>
Number of larvicide injections above this site	1	3	5	0		
Crustaceans	83.22b	0.44a	460.00c	102.87a	48.11	P<0.01
Siphonuridae	0.00a	0.00a	0.45a	0.82a	0.58	n.s.
Baetidae	637.26b	52.95a	268.77ab	463.52b	255.45	n.s.
Heptageniidae	400.79a	175.60a	994.41b	476.53b	427.55	P<0.05
Tricorythidae	57.08a	10.64a	45.77a	177.65b	47.75	n.s.
Caenidae	3.38a	0.26a	7.75a	16.31b	4.38	n.s.
Leptophlebiidae	1.22a	0.71a	0.00a	25.22a	2.16	P<0.05
Polymitarcyidae	11.76a	7.85a	2.48a	140.71a	14.36	p<0.01
EPHEMEROPTERA						
combined	1136.63b	270.02a	1357.31b	1369.88b	869.96	P<0.05
ODONATA	0.26a	0.00a	7.25b	2.30ab	1.42	n.s.
PLECOPTERA	19.38bc	5.14b	0.00a	74.68c	8.86	P<0.01
HEMIPTERA	0.00a	0.26a	24.88b	4.83ab	2.71	P<0.05
COLEOPTERA	1.22a	2.21a	2.96a	1.52a	1.90	n.s.
Hydropsychidae	442.61a	1418.06a	1478.11a	2093.11a	1179.32	n.s.
Hydroptilidae	0.00a	1.22a	1.76a	1.80a	1.04	n.s.
Leptoceridae	7.67a	9.83a	5.69a	10.08a	8.13	n.s.
Brachycentridae	0.91a	18.28b	0.00a	0.26a	1.61	P<0.01
TRICHOPTERA						
combined	449.82a	1461.18a	1509.08a	2112.49a	1204.04	n.s.
Simuliidae	57.82a	43.45a	41.43a	8.89a	31.37	n.s.
Tanypodinae	159.69ab	91.26a	284.76b	234.50ab	176.84	n.s.
Orthocladiinae	128.72a	37.73a	51.12a	31.89a	53.20	n.s.
Chironomini	869.96bc	161.93a	1240.65c	231.81ab	448.78	P<0.05
Tanytarsini	228.61a	14.49a	29.97a	48.09a	47.19	n.s.
Empididae	5.14a	5.14a	37.84a	3.95a	8.22	n.s.
DIPTERA combined	1495.24b	522.60a	1848.27b	575.77a	956.19	P<0.01
ACARI	12.11a	76.20ab	178.31b	18.68a	42.48	P<0.05
Gastropoda	18.90a	19.64a	22.11a	16.37a	19.15	n.s.
Pelecypoda	119.01a	127.23ab	615.03b	38.37a	138.00	n.s.
MOLLUSCA						
combined	150.36ab	162.31ab	689.24b	56.81a	176.42	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each year a set of five, 645 cm<sup>2</sup> samples were collected each week for three consecutive weeks.

<sup>(3)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.

TABLE 12. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED ABOUT ONE KM UPRIVER FROM SITE 3 (CECIL FERRY), NORTH SASKATCHEWAN RIVER, NORTH SIDE.

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(3)</sup>
Number of larvicide injections above this site	1	3	5	0		
Crustaceans	196.70b	9.84a	166.11b	136.40b	82.75	P<0.05
Siphonuridae	0.00	0.00	0.00	0.00	0.00	
Baetidae	301.27a	67.12a	60.90a	221.33a	128.75	n.s.
Heptageniidae	193.54a	89.78a	163.82a	287.40a	169.22	n.s.
Tricorythidae	15.94a	35.22ab	36.84ab	136.09b	41.27	n.s.
Caenidae	20.16a	12.00a	3.95a	2.45a	7.28	n.s.
Leptophlebiidae	0.00a	0.26a	2.45ab	31.17b	2.44	P<0.05
Polymitarcyidae	2.48a	9.23a	7.25a	33.12a	9.00	n.s.
EPHEMEROPTERA						
combined	553.63ab	285.42a	345.74a	834.60b	462.45	P<0.05
ODONATA	2.17ab	0.59a	0.59a	4.09b	1.53	n.s.
PLECOPTERA	5.14b	0.26a	0.00a	123.54c	4.57	P<0.01
HEMIPTERA	0.00a	0.26a	2.96a	5.14a	1.35	n.s.
COLEOPTERA	0.26a	0.26a	0.26a	0.59a	0.33	n.s.
Hydropsychidae	347.34a	1293.20b	4334.11c	2127.14bc	1427.89	P<0.01
Hydroptilidae	0.00a	2.14a	0.00a	2.53a	0.82	n.s.
Leptoceridae	0.26a	3.63a	1.22a	1.22a	1.32	n.s.
Brachycentridae	10.74a	3.67a	1.22a	0.82a	2.86	n.s.
TRICHOPTERA						
combined	366.28a	1323.34b	4344.10c	2141.89bc	1457.81	P<0.01
Simuliidae	8.91a	49.12a	21.76a	16.70a	20.14	n.s.
Tanypodinae	243.91a	23.77a	283.45a	139.93a	124.03	n.s.
Orthocladinae	144.55a	31.66a	108.40a	83.33a	80.47	n.s.
Chironomini	314.50ab	189.99ab	578.43b	79.72a	229.14	n.s.
Tanytarsini	114.61a	119.23a	59.53a	72.79a	87.72	n.s.
Empididae	1.22a	15.93a	7.67a	5.14a	5.69	n.s.
DIPTERA combined	876.00a	513.04a	1128.80a	433.51a	686.07	n.s.
ACARI	12.65a	19.46a	479.84b	56.81a	51.84	n.s.
Gastropoda	63.94b	4.09a	5.14a	12.65ab	11.90	n.s.
Pelecypoda	34.48a	13.60a	16.06a	24.67a	20.82	n.s.
MOLLUSCA						
combined	101.57a	15.83a	28.85a	46.97a	38.63	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each year a set of five, 645 cm<sup>2</sup> samples were collected each week for three consecutive weeks.

<sup>(3)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.

TABLE 13. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED FROM THE NORTH SASKATCHEWAN RIVER NORTH SIDE, ABOUT ONE KM UPRIVER FROM SITE 4 (THE CONFLUENCE)

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(3)</sup>
Number of larvicide injections above this site	3	3	6	1		
Crustaceans	0.00a	2.94a	204.73b	40.73b	12.56	P<0.01
Siphonuridae	0.00	0.00	0.00	0.00	0.00	
Baetidae	3.66a	9.69ab	10.42ab	342.72b	20.03	n.s.
Heptageniidae	5.99a	20.95a	6.61a	12.65a	10.23	n.s.
Tricorythidae	78.43ab	56.81ab	41.76a	145.22b	72.11	n.s.
Caenidae	0.00a	0.00a	1.76a	0.00a	0.29	n.s.
Leptophlebiidae	0.00a	22.04b	0.00a	4.52b	2.36	P<0.01
Polymitarcyidae	9.83a	3.95a	0.00a	6.13a	3.42	n.s.
EPHEMEROPTERA						
combined	149.66a	176.42a	83.33a	520.19b	148.35	P<0.05
ODONATA	0.00	0.00	0.00	0.00	0.00	
PLECOPTERA	1.22a	0.00a	0.00a	44.95b	2.18	P<0.01
HEMIPTERA	12.65b	0.00a	6.61b	0.00a	2.19	P<0.05
COLEOPTERA	0.00	0.00	0.00	0.00	0.00	
Hydropsychidae	529.88a	989.83b	1201.26b	1281.33b	947.42	P<0.05
Hydroptilidae	1.22a	33.03b	324.84c	0.00a	11.53	P<0.01
Leptoceridae	0.00a	0.00a	0.00a	1.22a	0.22	n.s.
Brachycentridae	0.00a	12.65b	25.44b	0.26a	3.62	P<0.01
TRICHOPTERA						
combined	533.56a	1036.53b	1583.89b	1284.29b	1029.39	P<0.01
Simuliidae	19.51a	9.99a	9.99a	45.88a	17.45	n.s.
Tanypodinae	208.41bc	39.83ab	250.77c	28.85a	88.54	P<0.05
Orthocladinae	476.53b	58.02a	886.16b	234.50ab	276.33	P<0.05
Chironomini	653.64a	315.96a	2778.71b	532.33a	743.73	P<0.01
Tanytarsini	366.28a	149.66a	1917.67b	125.18a	339.41	P<0.01
Empididae	3.33a	15.93ab	258.72b	3.95a	16.51	P<0.05
DIPTERA combined	1818.70b	637.26a	6250.73c	1022.29ab	1650.95	P<0.01
ACARI	27.58a	135.77a	873.98b	85.10a	129.92	P<0.01
Gastropoda	0.00a	6.61ab	1.22ab	19.30b	3.31	n.s.
Pelecypoda	16.06b	0.00a	2.48ab	14.62b	4.52	P<0.05
MOLLUSCA						
combined	16.06ab	6.61ab	2.96a	32.85b	10.48	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each year a set of five, 645 cm<sup>2</sup> samples were collected each week for three consecutive weeks.

<sup>(3)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.



TABLE 14. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED FROM THE SOUTH SASKATCHEWAN RIVER, SOUTH SIDE, ABOUT TWO KM UPRIVER FROM SITE 4 (THE CONFLUENCE).

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(3)</sup>
Number of larvicide injections this site	3	4	8	4		
Crustaceans	0.00a	10.61b	451.90c	180.13c	30.26	P<0.01
Siphonuridae	0.00	0.00	0.00	0.00	0.00	
Baetidae	68.02a	126.64ab	458.20b	611.35b	222.36	P<0.05
Heptageniidae	16.82a	20.13a	402.65b	62.10ab	54.72	n.s.
Tricorythidae	223.39a	178.06ab	439.55bc	943.06c	358.75	P<0.01
Caenidae	0.00a	1.76a	50.44b	0.00a	2.45	P<0.01
Leptophlebiidae	1.22a	22.91a	5.05a	0.00a	3.23	n.s.
Polymitarcyidae	0.00a	0.00a	13.92b	1.22ab	1.40	n.s.
EPHEMEROPTERA						
combined	332.43a	418.76a	1526.57b	1654.77b	769.90	P<0.01
ODONATA	0.00a	1.22a	2.45a	3.04a	1.36	n.s.
PLECOPTERA	0.00a	1.76a	11.08a	2.98a	2.39	n.s.
HEMIPTERA	0.00a	0.00a	0.00a	1.22a	0.22	n.s.
COLEOPTERA	0.00	0.00	0.00	0.00	0.00	
Hydropsychidae	237.78a	477.63ab	940.89ab	1065.60b	581.10	n.s.
Hydroptilidae	39.27a	10.89a	110.69ab	207.93b	56.81	n.s.
Leptoceridae	0.00a	0.00a	2.94a	1.76a	0.82	n.s.
Brachycentridae	1.22a	1.76a	0.00a	0.00a	0.57	n.s.
TRICHOPTERA						
combined	337.84a	526.23ab	1095.48ab	1317.26b	711.85	n.s.
Simuliidae	3.95a	111.49b	204.97b	163.55b	64.90	n.s.
Tanypodinae	167.27a	36.41a	27.97a	35.22a	49.70	n.s.
Orthocladiinae	104.93ab	83.92a	499.03bc	698.84c	236.14	P<0.05
Chironomini	565.24b	169.22a	366.28b	634.33b	386.26	P<0.01
Tanytarsini	447.75a	373.97a	549.81a	726.78a	508.33	n.s.
Empididae	0.00a	1.22ab	19.49b	26.50b	4.95	n.s.
DIPTERA combined	1335.60a	904.73a	1944.36a	2370.37a	1537.15	n.s.
ACARI	1149.80ab	1060.70a	2186.76bc	3242.40c	1716.19	P<0.05
Gastropoda	0.00a	0.00a	0.00a	1.22a	0.22	n.s.
Pelecypoda	5.14b	0.00a	0.59ab	0.00a	0.77	n.s.
MOLLUSCA						
combined	5.14a	0.00a	0.59a	1.22a	1.16	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each year a set of five, 645 cm<sup>2</sup> samples were collected each week for three consecutive weeks.

<sup>(3)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.

TABLE 15. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED ABOUT ONE KM UPRIVER FROM SITE 9 (GRONLID FERRY), MAIN SASKATCHEWAN RIVER, SOUTH SIDE.

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(4)</sup>
Number of larvicide injections above this site <sup>(3)</sup>	0 (6)	0 (7)	4 (18)	0 (5)		
Crustaceans	168.43a	347.34a	-	231.81a	238.33	n.s.
Siphonuridae	0.00	0.00	-	0.00	0.00	
Baetidae	190.87a	49.35a	-	40.40a	72.62	n.s.
Heptageniidae	375.70a	150.71a	-	211.81a	181.81	n.s.
Tricorythidae	33.12ab	21.23a	-	209.38b	53.20	n.s.
Caenidae	1.22a	0.00a	-	0.00a	0.31	n.s.
Leptophlebiidae	1.62a	0.00a	-	1.80a	0.94	n.s.
Polymitarcyidae	2.83a	2.96a	-	29.58a	6.74	n.s.
EPHEMEROPTERA						
combined	446.71ab	237.23a	-	694.02b	418.76	n.s.
ODONATA	0.00a	0.44a	-	0.00a	0.13	n.s.
PLECOPTERA	0.00a	0.00a	-	43.65b	2.55	P<0.01
HEMIPTERA	7.17a	0.00a	-	0.00a	1.01	n.s.
COLEOPTERA	3.95b	0.00a	-	0.00a	0.70	n.s.
Hydropsychidae	1620.81ab	1243.51a	-	2493.59b	1712.96	n.s.
Hydroptilidae	11.96b	0.00a	-	3.95ab	3.00	n.s.
Leptoceridae	1.76a	29.19b	-	0.00a	3.37	P<0.05
Brachycentridae	6.71ab	34.88b	-	0.59a	6.60	P<0.05
TRICHOPTERA						
combined	1670.09ab	1320.30a	-	2505.11b	1769.11	n.s.
Simuliidae	74.86a	49.93a	-	26.23a	46.21	n.s.
Tanypodinae	177.65a	75.21a	-	71.28a	98.54	n.s.
Orthoclaadiinae	169.73b	28.48b	-	1.22a	21.37	n.s.
Chironomini	400.79b	146.91ab	-	31.43a	123.45	P<0.05
Tanytarsini	81.70b	61.24b	-	3.95a	28.42	P<0.05
Empididae	8.46b	0.00a	-	0.00a	1.11	P<0.01
DIPTERA combined	938.72b	445.68b	-	154.60a	401.72	P<0.05
ACARI	106.65a	51.12a	-	313.77a	119.78	n.s.
Gastropoda	58.53a	25.56a	-	5.27a	20.48	n.s.
Pelecypoda	29.48a	60.38a	-	90.41a	54.46	n.s.
MOLLUSCA						
combined	90.62a	95.38a	-	123.45a	102.28	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each year a set of five, 645 cm<sup>2</sup> samples were collected each week for 3 consecutive weeks.

<sup>(3)</sup>Numbers in brackets indicate numbers of treatments in entire Saskatchewan River System above sampling site. Unbracketed numbers indicate numbers of treatments in Main Saskatchewan River alone.

<sup>(4)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.

TABLE 16. MEAN NUMBERS<sup>(1)</sup> OF AQUATIC INVERTEBRATES IN SURBER-NET SAMPLES<sup>(2)</sup> COLLECTED ABOUT ONE KM UPRIVER FROM SITE 9 (GRONLID FERRY), MAIN SASKATCHEWAN RIVER, NORTH SIDE.

Year	1977	1978	1979	1980	All years combined	Significance of difference between years <sup>(4)</sup>
Number of larvicide injections above this site <sup>(3)</sup>	0 (6)	0 (7)	4 (18)	0 (5)		
Crustaceans	216.77a	320.37a	-	678.20a	361.24	n.s.
Siphonuridae	0.00	0.00	-	0.00	0.00	
Baetidae	59.55a	6.97a	-	61.78a	30.17	n.s.
Heptageniidae	41.70a	8.66a	-	16.06a	18.16	n.s.
Tricorythidae	84.51ab	20.12a	-	224.42b	73.13	P<0.05
Caenidae	0.00	0.00	-	0.00	0.00	
Leptophlebiidae	0.26a	0.26a	-	0.26a	0.26	n.s.
Polymitarcyidae	6.27b	0.59a	-	0.26a	1.44	P<0.05
EPHEMEROPTERA						
combined	204.12ab	39.18a	-	338.63b	139.93	n.s.
ODONATA	0.00	0.00	-	0.00	0.00	
PLECOPTERA	0.26a	0.82a	-	6.61a	1.59	n.s.
HEMIPTERA	1.22a	0.00a	-	1.22a	0.70	n.s.
COLEOPTERA	0.26a	0.00a	-	0.00a	0.08	n.s.
Hydropsychidae	938.72b	90.20a	-	352.18ab	310.89	n.s.
Hydroptilidae	0.00a	2.14a	-	0.26a	0.58	n.s.
Leptoceridae	23.09b	1.80a	-	0.00a	3.07	P<0.01
Brachycentridae	13.77b	1.62a	-	0.82a	3.11	P<0.05
TRICHOPTERA						
combined	985.28b	99.93a	-	353.81ab	327.10	n.s.
Simuliidae	23.67a	96.36a	-	2.71a	19.73	n.s.
Tanypodinae	133.52a	13.92a	-	13.13a	29.49	n.s.
Orthocladiinae	119.86a	7.69a	-	5.99a	18.43	n.s.
Chironomini	646.14b	42.45a	-	49.35a	111.20	P<0.01
Tanytarsini	344.14a	18.19a	-	43.46a	65.53	n.s.
Empididae	3.95a	1.22a	-	0.00a	1.22	n.s.
DIPTERA combined	1347.96b	227.56ab	-	146.23a	355.45	n.s.
ACARI	108.90ab	85.90a	-	362.92b	150.71	n.s.
Gastropoda	84.33b	5.95a	-	0.00a	7.40	P<0.01
Pelecypoda	7.08a	16.60a	-	10.39a	10.74	n.s.
MOLLUSCA						
combined	92.30b	30.00ab	-	10.39a	31.06	n.s.

<sup>(1)</sup>Geometric means calculated from  $\log_{10}(x + 1)$  values.

<sup>(2)</sup>In each week a set of five, 645 cm<sup>2</sup> samples were collected each week for 3 consecutive weeks.

<sup>(3)</sup>Numbers in brackets indicate numbers of treatments in entire Saskatchewan River System above sampling site. Unbracketed numbers indicate numbers of treatments in Main Saskatchewan River alone.

<sup>(4)</sup>Calculated from  $\log_{10}(x + 1)$  values. Means followed by different letters, differ significantly (P<0.05) as indicated by Duncan's New Multiple Range tests.

TABLE 17. SUMMARY OF TABLES 11 TO 16, INCLUSIVE, IDENTIFYING THOSE YEARS WHICH PROVIDED MAXIMUM DENSITIES OF BENTHIC INVERTEBRATES IN EACH OF THE SIX LOCATIONS IN THE NORTH, SOUTH, AND MAIN BRANCHES OF THE SASKATCHEWAN RIVER<sup>(1)</sup>

Site Number	3	3	4	4	9	9
River Branch	North	North	North	South	Main	Main
River Side	South	North	North	South	South	North
Notes	EFFLUENT <sup>(2)</sup>					
1979 DATA MISSING <sup>(3)</sup>						
CRUSTACEANS	1979 (143) (HS)	1977 (61) (S)	1979 (64) (HS)	1979 (140) (HS)	1978 (108)	1980 (211)
Siphonuridae	1980 (0.25)	— —	— —	— —	— —	— —
Baetidae	1977 (198)	1977 (93)	1980 (106)	1980 (189) (S)	1977 (59)	1980 (19)
Heptageniidae	1979 (309) (S)	1980 (89)	1978 (6.5)	1979 (125)	1977 (117)	1977 (13)
Tricorythidae	1980 (55)	1980 (42)	1980 (45)	1980 (293) (HS)	1980 (65)	1980 (70) (S)
Caenidae	1980 (5.1)	1977 (6.2)	1979 (0.55)	1979 (16) (HS)	1977 (0.38)	
Leptophlebiidae	1980 (7.8) (S)	1980 (9.7) (S)	1978 (6.8) (HS)	1978 (7.1)	1980 (0.56)	means alike (0.08)
Polymitarcyidae	1980 (44) (HS)	1980 (10)	1977 (3.1)	1979 (4.3)	1980 (9.2)	1977 (1.9) (S)
EPHEMEROPTERA (combined)	1980 (425) (S)	1980 (259) (S)	1980 (162) (S)	1980 (514) (HS)	1980 (215)	1980 (105)
ODONATA	1979 (2.2)	1980 (1.3)	- -	1980 (0.94)	1978 (0.14)	
PLECOPTERA	1980 (23) (HS)	1980 (38) (HS)	1980 (14) (HS)	1979 (3.4)	1980 (14) (HS)	1980 (2.1)
HEMIPTERA	1979 (8) (S)	1980 (1.6)	1977 (3.9) (S)	1980 (0.38)	1977 (2.2)	1977 (0.38)
COLEOPTERA	1979 (0.92)	1980 (0.18)	- -	- -	1977 (1.2)	1977 (0.08)
Hydropsychidae	1980 (648)	1979 (1346) (HS)	1980 (388) (S)	1980 (331)	1980 (773)	1977 (291)
Hydroptilidae	1980 (0.56)	1980 (0.78)	1979 (101) (HS)	1980 (64)	1977 (3.7)	1978 (0.66)
Leptoceridae	1980 (3.1)	1978 (1.1)	1980 (0.38)	1979 (0.91)	1978 (9.0) (S)	1977 (7.2) (HS)

(continued on next page)

Table 17 (continued)

Site Number	3	3	4	4	9	9
River Branch	North	North	North	South	Main	Main
River Side	South	North	North	South	South	North
Notes	EFFLUENT <sup>(2)</sup>					
1979 DATA MISSING <sup>(3)</sup>						
Brachycentridae	1978 (5.7) (HS)	1977 (3.3)	1979 (7.9) (HS)	1978 (0.55)	1978 (11) (S)	1977 (4.3) (S)
TRICHOPTERA (combined)	1980 (656)	1979 (1349) (HS)	1979 (491) (HS)	1980 (408)	1980 (777)	1977 (306)
Simuliidae	1977 (18)	1978 (15)	1980 (14)	1979 (64)	1977 (23)	1978 (30)
Tanypodinae	1979 (88)	1979 (88)	1979 (78) (S)	1977 (52)	1977 (55)	1977 (41)
Orthocladiinae	1977 (40)	1977 (45)	1979 (275) (S)	1980 (217) (S)	1977 (53)	1977 (37)
Chironomini	1979 (385) (S)	1979 (180)	1979 (862) (HS)	1980 (197) (HS)	1977 (124) (S)	1977 (201) (HS)
Tanytarsini	1977 (71)	1978 (36)	1979 (594) (HS)	1980 (226)	1977 (25) (S)	1977 (107)
Empididae	1979 (12)	1978 (4.9)	1979 (80) (S)	1980 (8.2)	1977 (2.6) (HS)	1977 (1.2)
DIPTERA (combined)	1979 (573) (HS)	1979 (350)	1979 (1940) (HS)	1980 (736)	1977 (291) (S)	1977 (418)
ACARI	1979 (55) (S)	1979 (149)	1979 (271) (HS)	1980 (1015) (S)	1980 (97)	1980 (112)
Gastropoda	1979 (6.9)	1977 (20)	1980 (6.0)	1980 (0.38)	1977 (18)	1977 (26) (HS)
Pelecypoda	1979 (191)	1977 (11)	1980 4.5(S)	1977 (1.6)	1980 (28)	1978 (5.1)
MOLLUSCA (combined)	1979 (214)	1977 (32)	1980 (10)	1977 (1.6)	1980 (38)	1977 (29)

<sup>(1)</sup>Notations in parentheses indicate annual mean (number/m<sup>2</sup>) (geometric, calculated from  $\log^{10} (n + 1)$  transformations), and also indicate whether differences between the four years were significant (S) or highly significant (HS).

<sup>(2)</sup>Samples from this location were collected nine km downstream from a pulp mill (newsprint), directly in the effluent path.

<sup>(3)</sup>No samples were collected from Site Nine in 1979.

samples collected there in 1979). Differences between years were not significant in either site.

Tricorythids (almost 100 percent *Tricorythodes minutus* Traver), the third of three ephemeropteran families most abundantly represented, peaked in 1980 in all six locations. Differences between years were highly significant in the South Saskatchewan River and significant in one location in the main Saskatchewan River.

Larvae of all three of these families are considered to be swimmers, climbers, and clingers, and feed by collecting and scraping detritus, diatoms, etc. from substrates (Table 5). Fredeen *et al.* (1975) showed that methoxychlor was rapidly adsorbed to solids in river water. Thus these larvae could have been exposed to methoxychlor either or both as a contact or stomach poison. Despite this they appeared to resist harmful effects.

The less abundant caenids (about 98 percent *Caenis tardata* McDunnough) and leptophlebiids (about 100 percent *Traverella albertana* (McDunnough)) which possessed similar living and feeding habits, and filter-feeding siphonurids (about 100 percent *Isonychia sicca*) also peaked in the North Saskatchewan River in one or more locations in 1980, in the South Saskatchewan in 1978 (leptophlebiids) and 1979 (caenids) with highly significant differences between years, and in the main Saskatchewan River in 1977 (caenids) and 1980 (leptophlebiids), with differences between years not significant.

Burrowing polymitarcyids (100 percent *Ephoron album* (Say)) peaked in the North Saskatchewan River in two locations in 1980, with highly significant differences between years in one location. They also peaked in the South Saskatchewan River in 1979 and in the main Saskatchewan River (south side) in 1980.

Mean August populations of Plecoptera, all taxa combined, peaked in five of the six locations in 1980 ( $P < 0.01$  in four locations), and peaked in the sixth location (the South Saskatchewan River), in 1979. Larvae were scarce however, peaking at 38 or fewer larvae per  $m^2$  of river bed (Table 17). Larvae of *Isoperla* would not have hatched until after the August collection dates each year.

Larvae of Odonata and Coleoptera were generally present although rare (absent from some sites) and significant trends in numbers were not evident.

Immature hemipterans (corixids) also were relatively scarce in most sites but numbers peaked in two rivers in 1980 and in the main Saskatchewan River in 1977. Samples were not collected there in 1979. Corixids migrate from surrounding regions to overwinter in the rivers.

Mean numbers of trichopteran larvae, all taxa combined, peaked in one or more locations in all three rivers in 1980. In two of the three locations in the North Saskatchewan River, however, peaks occurred in 1979 with differences between years highly significant. Ninety-eight percent of the trichopterans were hydropsychids which, because of their size and number, easily comprised the most important portion of the total invertebrate biomass of the river. Sixty to 90 percent of the hydropsychids were *Cheumatopsyche* spp. and the remainder were mainly *Hydropsyche alternans* (Walker) and *H. confusa*. It had been thought that filter-feeding hydropsychid larvae (Table 5) might have been relatively sensitive to methoxychlor which is known to readily adsorb to particles suspended in the water (Fredeen *et al.*, 1975). However, population numbers showed no indication of this.

Larvae of three other families of Trichoptera, the Hydroptilidae (*Mayatrichia ayama* Mosely), Leptoceridae (*Nectopsyche diarina* (Ross)), and Brachycentridae (*Brachycentrus occidentalis* Banks), all considered to be herbivores (Table 5), were relatively scarce. In the North and South Saskatchewan Rivers their populations peaked in either 1979 or 1980. The one exception was Brachycentridae in the South Saskatchewan, peaking in 1978. In the main

Saskatchewan River they peaked in 1977 or 1978. However, no samples were collected there in 1979, which could have been their peak year as in the other rivers.

Larvae of Diptera, of which about 98 percent were chironomids, peaked in all three benthic sampling locations in the North Saskatchewan River in 1979, with differences between years highly significant in two locations. Numbers peaked in the South Saskatchewan in 1980 and in the main Saskatchewan in 1977 (samples were not collected in 1979) and differences between years were significant in one North Saskatchewan location.

Of the Chironomidae about 50 to 75 percent of the specimens were species of Chironomini, a subfamily with many filter-feeders, but otherwise with very diverse living and feeding habits (Table 5). In the North Saskatchewan River numbers of Chironomini peaked in 1979, and in the South Saskatchewan in 1980 with significant or highly significant differences between years in three of the four sampling locations.

Larvae of the less abundant predaceous Tanypodini peaked in the three North Saskatchewan River locations in 1979, with differences between years significant in one location, and peaked in the South and main Saskatchewan Rivers in 1977 with non-significant differences between years.

Larvae of the herbivorous Orthocladiinae peaked in 1979 and 1980 in the North and South Saskatchewan Rivers at Site 4 with significant differences between years but elsewhere showed non-significant trends. Larvae of Tanytarsini peaked in 1979 in the North Saskatchewan River (Site 4) with highly significant differences between years and in the South Saskatchewan (Site 4) in 1980. Elsewhere populations did not trend significantly.

Trends in the relatively small populations of Empididae and Simuliidae were generally inconclusive but peaked in the North Saskatchewan River in 1977 or 1980, in the South Saskatchewan River in 1979 or 1980 and in the main Saskatchewan River in 1977 or 1978 (where no benthic samples were collected in 1979).

Mites, whose larvae are parasitic, and adults are predators of various aquatic invertebrates, peaked in all three locations in the North Saskatchewan River in 1979 (with significant or highly significant differences between years in two locations). They peaked in the South Saskatchewan River in 1980 (with significant differences between years), and in the main Saskatchewan River in 1980 (with non-significant differences between years). These trends provide indirect evidence that numbers of their prey species also may have increased in abundance during these four years.

Molluscs were scarce in most locations and trends in numbers were not significant.

Thus in general, data from benthic samples collected each August from all three branches of the Saskatchewan River System indicated that with few exceptions populations of non-simuliid taxa increased rather than decreased throughout three years of increasingly intensive use of methoxychlor black fly larvicide followed by a fourth year of less intensive use.

### **Check-list of taxa in benthic samples**

A detailed list of taxa (Table 18) was prepared from benthic samples collected in 1980. (Samples collected in earlier years were not analyzed in such detail because of inadequate systematic keys. However, samples from previous years are being retained in the event that re-examinations in greater detail are required.)

These benthic samples would not have contained species which would have been in the egg stage in August, particularly some heptageniid mayflies and some plecopterans. But data in Table 18 show that sufficient other taxa were present in some or all locations sampled to

TABLE 18. LIST OF INVERTEBRATE TAXA COLLECTED IN SURBER-TYPE NETS FROM SIX SITES IN THE NORTH, SOUTH, AND MAIN BRANCHES OF THE SASKATCHEWAN RIVER IN SASKATCHEWAN, AUGUST 5, 12, AND 19, 1980<sup>(1)</sup> (2).

Saskatchewan River Branch	North	North	North	South	Main	Main
Site <sup>(3)</sup>	Above Site #3		Above Site #4		Above Site #9	
River Margin	North	South	North	South	North	South
CONCHOSTRACA	0	0	X	0	0	0
CLADOCERA	X	X	0	X	0	0
OSTRACODA	X	X	X	X	X	X
COPEPODA	X	X	X	X	0	0
MALACOSTRACA						
AMPHIPODA: <i>Hyalella azteca</i>	0	0	0	X	0	0
INSECTA						
EPHEMEROPTERA						
Siphonuridae:						
<i>Isonychia sicca</i>	X	X	0	0	0	0
Baetidae: <i>Baetis insignificans</i>	0	X	X	X	X	X
<i>B. tricaudatus</i>	0	X	X	X	X	X
<i>Baetis</i> nr. <i>pluto</i>	X	X	X	X	X	X
<i>Baetis</i> sp.	X	X	X	X	X	0
<i>Centroptilum bifurcatum</i>	0	0	0	0	X	0
<i>Pseudocloeon</i> sp.	X	X	0	X	X	0
Heptageniidae:						
<i>Heptagenia adequata</i>	0	0	0	0	0	X
<i>H. elegantula</i>	0	X	0	0	0	X
<i>H. pulla</i>	0	X	0	X	0	X
<i>Heptagenia</i> sp.	X	X	0	X	X	X
<i>Stenonema terminatum</i>	X	X	X	X	X	X
Tricorythidae:						
<i>Tricorythodes</i>						
<i>corpulentus</i>	0	0	0	0	0	X
<i>T. minutus</i>	0	X	0	X	0	X
<i>Tricorythodes</i> sp.	X	X	X	X	X	X
Caenidae: <i>Caenis tardata</i>	X	X	0	0	0	0
Leptophlebiidae:						
<i>Traverella albertana</i>	X	X	X	0	X	X
Polymitarcyidae:						
<i>Ephoron album</i>	X	X	X	0	X	X

(continued on next page)



Table 18 (continued)

Saskatchewan River Branch	North	North	North	South	Main	Main
Site <sup>(3)</sup>	Above Site #3		Above Site #4		Above Site #9	
River Margin	North	South	North	South	North	South
ODONATA						
Anisoptera:						
<i>Ophiogomphus severus</i>	X	X	0	X	0	0
Zygoptera: <i>Ischnura</i> sp.	0	0	0	X	0	0
PLECOPTERA (Immatures)	X	X	X	X	X	X
Pteronarcyidae:						
<i>Pteronarcys dorsata</i>	0	0	0	X	0	0
Perlidae:						
<i>Acroneuria abnormis</i>	X	0	0	0	0	0
HEMIPTERA						
Corixidae (Immatures)	X	X	0	X	X	0
COLEOPTERA						
Dytiscidae: <i>Deronectes</i> sp.	X	X	0	0	0	0
Helodidae (Immatures)	0	X	0	0	0	0
TRICHOPTERA						
Psychomyiidae:						
<i>Psychomyia flavida</i>	0	X	0	0	0	0
Polycentropodidae:						
<i>Neureclipsis bimaculata</i>	0	0	0	0	0	X
Hydropsychidae:						
<i>Hydropsyche alternans</i>	X	X	X	X	X	X
<i>H. placoda</i>	X	X	X	X	X	X
<i>H. occidentalis</i>	0	0	0	X	0	0
<i>H. confusa</i>	X	X	X	0	X	X
<i>Cheumatopsyche</i> sp.	X	X	X	X	X	X
Hydroptilidae:						
<i>Hydroptila ajax</i>	X	0	0	X	0	0
<i>Mayatrichia ayama</i>	X	X	0	X	X	X
Brachycentridae:						
<i>Brachycentrus</i>						
<i>occidentalis</i>	X	X	X	0	X	X
Leptoceridae:						
<i>Ceraclea tarsipunctata</i>	0	X	0	X	0	X
<i>Nectopsyche diarina</i>	0	X	X	0	0	X
<i>Oecetis avara</i>	0	X	0	0	0	0
Unidentified sp.	X	X	0	0	0	

(continued on next page)

Table 18 (continued)

Saskatchewan River Branch	North	North	North	South	Main	Main
Site <sup>(3)</sup>	Above Site #3		Above Site #4		Above Site #9	
River Margin	North	South	North	South	North	South
<b>DIPTERA:</b>						
Simuliidae:						
<i>Simulium luggeri</i>	X	X	X	X	X	X
<i>S. meridionale</i>	X	X	X	0	X	0
<i>S. vittatum</i>	X	X	X	X	0	X
Chironomidae:						
Chironominae						
Chironomini:						
(unidentified)	X	X	X	X	X	X
<i>Chironomus</i> (s.s.) sp.	X	X	X	0	0	0
<i>Cryptochironomus</i> sp.	0	X	X	0	0	X
<i>Microtendipes</i> sp.	X	X	X	X	X	X
<i>Paracladopelma</i> sp.	0	X	0	0	0	0
<i>Polypedilum</i> sp.	X	X	X	X	X	X
<i>Robachia</i> sp.	0	X	0	0	0	0
Tanytarsini (unidentified)	X	X	X	X	X	X
<i>Rheotanytarsus</i> sp.	X	X	0	0	X	0
Orthocladiinae (unidentified)	X	X	X	X	X	X
<i>Cricotopus</i> (s.s.) sp.	0	0	0	X	0	X
<i>Tvetenia</i> sp.	0	0	0	X	0	X
Tanypodinae (unidentified)	X	X	X	X	X	X
<i>Thienemannimyia</i> sp.	X	X	X	X	X	X
<b>ACARI</b>						
Parasitengona	X	X	X	X	X	X
<b>MOLLUSCA</b>						
GASTROPODA (unidentified)	0	0	0	0	0	X
Ancylidae	X	X	X	0	0	0
Limnaeidae	0	X	0	0	0	0
Physidae	0	0	0	X	0	0
Planorbidae	X	X	X	0	0	0
<b>PELECYPODA</b>						
Sphaeriidae	X	X	X	0	X	X

(1)On each of the three dates, five 645 cm<sup>2</sup> river bed samples were collected from each of the six sites. The diameter of the mesh openings in the net was 0.2 mm.

(2)"0" = absent in samples; "X" = present

(3)See Fig. 1 to locate sites on map, and Table 1 for distances.

indicate that a complex invertebrate fauna still existed following four years of relatively intensive use of methoxychlor black fly larvicide. Included were representatives of widely varied life cycles, larval activity patterns, and feeding habits (Table 5). Particularly abundant and/or widespread in 1980 were mayfly larvae (especially the clinging, herbivorous heptageniids, tricorythids, and leptophlebiids); swimming herbivores (baetids); carnivorous odonatids; herbivorous stoneflies; filter-feeding, herbivorous or detritivorous hydropsychids; herbivorous hydroptilids, brachycentrids, and leptocerids; filter-feeding simuliids and chironomids (many taxa); herbivorous and predatory chironomids (tanypodines and orthocladiines); parasitic mites and various molluscs.

Included also were species with life cycles as short as four to five weeks (especially *S. luggeri* or others with larvae continuously abundant throughout the summer (heptageniids and other mayfly taxa, hydropsychids and many chironomids)), and species with life cycles lasting one or more years (pteronarcid and perlid stoneflies). With repeated insecticide treatments throughout four consecutive summers one might have expected that species with relatively short life cycles such as simuliids would have become relatively more abundant in comparison with species which spent longer periods as larvae. However, there was no evidence of this occurring and in fact simuliid larvae, excluding *S. vittatum*, became less abundant in successive years and differences between years were highly significant, at least in mid-river sites (Table 9), whereas species which spent much of each summer as larvae, such as many ephemeropterans, trichopterans, and chironomids, either peaked in the third or fourth years of the tests or trended insignificantly between years (Tables 6, 7, and 8).

### Need for Control of Black Flies at Sites of Breeding

Throughout four consecutive years of tests with methoxychlor as a black fly larvicide in the Saskatchewan River system in Saskatchewan, populations of larvae of the problem species of black fly, *S. luggeri* declined progressively to their lowest levels ( $P < 0.01$ ) in the final year (Table 9). Residents in east-central Saskatchewan experienced major outbreaks in 1976, 1977 and 1978 but almost complete relief from black fly outbreaks during 1979 and 1980. Maximum use of larvicide occurred in 1979, both as regards numbers of sites and numbers of injections. Also, in 1979, the main Saskatchewan River below the confluence of the two branches was injected for the first time. Greatly reduced populations of *S. luggeri* larvae throughout 1980 allowed reductions in numbers of treatments that year (Tables 2, 3, 4).

Provincial and Federal Departments of the Environment are rightfully concerned about the invertebrate fauna of the Saskatchewan River when renewals of permits for larviciding are requested each year. Data presented in this paper should help to rationalize those concerns. At the same time there has to be concern for human environments in some one to three million ha of land sometimes blanketed by widespread, prolonged outbreaks of *S. luggeri*. Not only were people unable to work out-of-doors during outbreaks in 1976 through 1978 unless well protected, but also livestock owners incurred considerable financial losses (Fredeen, 1981).

Despite many years of research towards protecting livestock individually from black fly attacks, both in this country and elsewhere, there still are no practical or economical means of protection available, especially for animals in large pastures. Within the region affected by outbreaks of *S. luggeri* in east-central Saskatchewan (up to three million ha in 1978) there are estimated to be more than 250,000 beef and dairy cattle in community and private pastures each summer. Most of these animals could not be regularly rounded up for insecticide treatments, even if durable, registered insecticides were available, because management and

chemical costs would be prohibitive. Labour and chemical costs are more efficiently used if infestations of black fly larvae are reduced when in their relatively limited river environments, rather than by attempting to reduce numbers of adults that have dispersed widely into the countryside. Furthermore, dispersals of adult black flies are affected by varying weather conditions which frequently catch livestock producers unprepared.

Thus at this time, black fly larviciding with methoxychlor remains the most practical method for minimizing damage from widespread outbreaks of *S. luggeri* from the Saskatchewan River, and this study shows that larviciding throughout a four-year period was relatively harmless to the natural environment of that river in the long term.

Alternatively one might consider reducing numbers of larvae of *S. luggeri* by reversing whatever ecological trends in the river system may have encouraged invasion by populations of this species in the early 1970's, and proliferation within a few years to the extent that widespread outbreaks of economic proportions were possible. Other haematophilic species of black flies such as *S. meridionale*, *S. venustum*, and *S. tuberosum* recently have become established in this river and may also require control in future years (Fredeen, 1981). Thus one might consider attempting to reverse recent ecological trends but such a "biological control" method would also affect the present day environments of non-simuliid taxa.

## CONCLUSIONS

Trends in numbers of non-simuliid invertebrates throughout 1977 to 1980 in the North, South, and main branches of the Saskatchewan River in Saskatchewan were generally directly related to the numbers of methoxychlor larvicide injections each year. Thus when total numbers of larvicide injections were increased from one in 1976, to six in 1977, seven in 1978, 19 in 1979, and five in 1980, densities of most non-simuliid taxa in benthic samples also peaked either in 1979 or 1980, many significantly so (Table 17). Mean numbers of total non-simuliids in all mid-river sites combined, also peaked in 1979 ( $P < 0.01$ ) (Table 9). Thus numbers of non-simuliid aquatic invertebrates showed similar upward trends during these years whether collected with artificial substrates from mid-river, or with Surber-type nets from benthic sites along the river margins.

Repopulation of treated sections was assured by drift of invertebrates downstream from extensive untreated sections, as well as by hatching of eggs and by movement of larvae from protected niches within each treated section. The abundant and complex benthic fauna surviving along the river margins presumably served as a rich source of emigrants for depopulated areas.

Some observed increases appear also to have been due to downstream displacements of larvae which had been stimulated to release during larvicide treatments.

Qualitatively also, the non-simuliid fauna appeared healthy at the conclusion of tests in 1980 (Table 18). Benthic samples collected from all three river branches throughout August that year contained a variety of species representing normal ranges of activity patterns, feeding habits, and life cycles. Although data in Tables 6 through 17 relate mainly to suprageneric taxa, qualitative analyses showed each of these taxa to be represented by relatively few dominant species throughout the four years of tests. Thus upward trends in numbers throughout two or more of the four years of treatments were caused mainly by increases in the numbers of relatively few species.

The fact that significant upward trends in numbers of most suprageneric taxa occurred during three years of increasingly intensive use of methoxychlor and a fourth year of less intensive use suggests that long-term effects of this larvicide on numbers of most non-simuliids were essentially neutral when compared with effects of natural ecological processes.

In general, this study of trends in quantities and qualities of invertebrate taxa inhabiting the three branches of the Saskatchewan River throughout four years of injections of methoxychlor larvicide indicates that *S. luggeri* may be successfully controlled in a limited portion of the Saskatchewan River without permanently harming major non-simuliid taxa. The results support data from an earlier study (Fredeen, 1975) which showed relatively rapid repopulation of a 160-km section of the Saskatchewan River following a single injection of methoxychlor.

#### ACKNOWLEDGEMENTS

I am greatly indebted to Richard and Lesley Moffatt whose steady persistence and careful work throughout the past five years helped to bring this huge project to completion. I am also indebted to D. Lehmkuhl, Peter Mason, Eric Whiting, and Douglas Smith for providing systematic expertise whenever required. Frequent consultations with Dr. J. R. Jowsey throughout the project were also very helpful. David Spurr prepared computer programs for the statistical analyses and Drs. Alfred Arthur and H. T. Fredeen provided suggestions for preparation of the manuscript. I thank Dr. G. Seguin-Swartz for the French version of the abstract.

#### REFERENCES

- Anderson, R.L., and D.L. DeFoe. 1980. Toxicity and bioaccumulation of endrin and methoxychlor in aquatic invertebrates and fish. *Environmental Pollution* 22:111–121.
- Butler, G.L., T.R. Deason, and J.C. O'Kelley. 1975. Loss of five pesticides from cultures of 21 planktonic algae. *Bulletin of Environmental Contamination and Toxicology*. 13:149–152.
- Corbet, P.S., F. Schmid, and C.L. Augustin. 1966. The Trichoptera of St. Helen's Island, Montreal. I: The species present and their relative abundance at light. *The Canadian Entomologist* 98:1284–1298.
- Cummins, K.W. 1973. Trophic relations of aquatic insects. *Annual Review of Entomology*. 18:183–206.
- Cummins, K.W. and G.F. Edmunds. 1978. Summary of ecological and distributional data for Ephemeroptera (mayflies);77–80. *In* An introduction to aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque.
- Cummins, K.W. and P.P. Harper. 1978. Summary of ecological and distributional data for Plecoptera (stoneflies);115–118. *Ibid*.
- Cummins, K.W. and G.B. Wiggins. 1978. Summary of ecological and distributional data for Trichoptera (caddisflies);175–185. *Ibid*.
- Cummins, K.W. and W.P. Coffman. 1978. Summary of ecological and distributional data for Chironomidae (Diptera);370–376. *Ibid*.
- Edwards, W.M. and B.L. Glass. 1971. Methoxychlor and 2,4,5-T in lysimeter percolation and runoff water. *Bulletin of Environmental Contamination and Toxicology*. 6:81–84.
- Environment Canada. 1978. Surface water data, Saskatchewan, 1977. Minister of Supply and Services, Canada; 188 pages.
- Environment Canada. 1979. Surface water data, Saskatchewan, 1978. *Ibid*. 190 pages.

- Environment Canada. 1980. (a) Surface water data, Saskatchewan, 1979. *Ibid.* 192 pages.
- Environment Canada. 1980. (b) Historical streamflow summary, Saskatchewan, to 1979. *Ibid.* 339 pages.
- Environment Canada. 1981. Surface water data, Saskatchewan, 1980. *Ibid.* 188 pages.
- Fredeen, F.J.H. 1969. Outbreaks of the black fly *Simulium arcticum* Malloch in Alberta. *Quaestiones Entomologicae* 5:341–372.
- Fredeen, F.J.H. 1972. Reactions of the larvae of three rheophilic species of Trichoptera to selected insecticides. *Canadian Entomologist* 104:945–953.
- Fredeen, F.J.H. 1974. Tests with single injections of methoxychlor black fly (Diptera: Simuliidae) larvicides in large rivers. *Ibid.* 106:285–305.
- Fredeen, F.J.H. 1975. Effects of a single injection of methoxychlor black fly larvicide on insect larvae in a 161-km (100 mile) section of the North Saskatchewan River. *Ibid.* 107:807–817.
- Fredeen, F.J.H. 1977. Some recent changes in black fly populations in the Saskatchewan River system in Western Canada coinciding with the development of reservoirs. *Canadian Water Resources Journal* 2:90–102.
- Fredeen, F.J.H. 1981. Keys to the black flies (Simuliidae) of the Saskatchewan River in Saskatchewan. *Quaestiones Entomologicae* 17:189–210.
- Fredeen, F.J.H., J.G. Saha and M.H. Balba. 1975. Residues of methoxychlor and other chlorinated hydrocarbons in water, sand and selected fauna following injections of methoxychlor black fly larvicide into the Saskatchewan River, 1972. *Pesticides Monitoring Journal* 8:241–246.
- Fredeen, F.J.H. and D.T. Spurr. 1978. Collecting semi-quantitative samples of black fly larvae (Diptera: Simuliidae) and other aquatic insects from large rivers with the aid of artificial substrates. *Quaestiones Entomologicae* 14:411–431.
- Fremling, C.R. 1960(a). Biology of a large mayfly *Hexagenia bilineata* (Say) of the upper Mississippi River. Iowa State University, Research Bulletin 482, Ames, Iowa.
- Fremling, C.R. 1960(b). Biology and possible control of nuisance caddisflies of the upper Mississippi River. Iowa State University, Research Bulletin 483, Ames, Iowa.
- Merritt, R.W. and K.W. Cummins. 1978. An introduction to the aquatic insects of North America. 441 pp. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- Muirhead-Thomson, R.C. 1973. Laboratory evaluation of pesticide impact on stream invertebrates. *Freshwater Biology* 3:479–498.
- Munroe, E.G. 1951. Pest Trichoptera at Fort Erie, Ontario. *Canadian Entomologist* 83:69–72.
- Paris, D.F., and D.L. Lewis. 1976. Accumulation of methoxychlor by microorganisms isolated from aqueous systems. *Bulletin of Environmental Contamination and Toxicology*. 15:24–32.
- Peterson, D.J. 1952. Observations on the biology and control of pest Trichoptera at Fort Erie, Ontario. *Canadian Entomologist* 84:103–107.
- Sebastien, R.J., and W.L. Lockhart. 1981. The influence of formulation of toxicity and availability of a pesticide (methoxychlor) to black fly larvae (Diptera: Simuliidae), some non-target aquatic insects and fish. *Ibid.* 113:281–293.
- Ward, H.B. and G.C. Whittaker. (Editor, W.T. Edmondson). 1959. Fresh-water biology. 1248 pp. John Wiley and Sons, New York, U.S.A.
- Wiggins, G.B. 1977. Larvae of North American caddisfly Genera (Trichoptera). 401 pp. University of Toronto Press, Toronto, Canada.

# CYMINDINE LEBIINI OF AUTHORS: REDEFINITION AND RECLASSIFICATION OF GENERA (CLEOPTERA: CARABIDAE)

George E. Ball  
Department of Entomology  
University of Alberta  
Edmonton, Alberta  
Canada T6G 2E3

Gerald J. Hilchie  
Department of Entomology  
University of Alberta  
Edmonton, Alberta  
Canada T6G 2E3

*Quaestiones Entomologicae*  
19: 93-216 1983

## ABSTRACT

Based on examination of character states of adults (in particular, sclerites of the ovipositor) of a limited sample of taxa, heretofore included in the lebiine subtribe Cymindina (= Tribes Cymindina and Pseudomasoreini, or Subfamily Cyminditae of authors), the following tribes and subtribes were found to be represented: Tribe Pterostichini, subtribe Platynina; Tribe Lachnophorini; Tribe Lebiini, Subtribes Pericalina, Apenina, Cymindina, Calleidina, and Dromiina; and Tribe Zuphiini. The South African *Anarmosta Péringuey*, 1896 (= *Euplynes* Schmidt-Goebel, 1846) is confirmed as a platynine. The New World tropical and subtropical *Eucaerus* LeConte, 1853 and *Lachnaces* Bates, 1872, are included in the *Eucaerus* complex, and transferred to the *Lachnophorini*. *Eucaerus* and *Lachnaces* are regarded as congeneric subgenera (new rank). Also included in the *Eucaerus* complex are the Neotropical genera *Asklepia* Liebke, 1938, and *Phaedrusium* Liebke, 1951. Transferred to the subtribe *Pericalina* are the Afrotropical (South African) *Leptosarcus Péringuey*, 1896, and (East African montane) *Selenoritus Alluaud*, 1917, the latter included as a subgenus of *Thyreopterus* Dejean, 1831 (new rank). Transferred to the subtribe *Apenina* are three genera: the New World *Apenes* LeConte, 1851, with subgenera *Apenes* sensu stricto (= *Malisus* Motschulsky, 1864), and *Sphalera* Chaudoir, 1875 (= *Didymochaeta* Chaudoir, 1875, new synonymy); Palaeartic *Trymosternus* Chaudoir, 1873; and the Old World Tropical Cymindoidea *Castelnau*, 1832. The latter genus includes as subgenera Cymindoidea (sensu stricto), *Platytarus* Fairmaire, 1850 (new rank), and *Habutarus* new subgenus (generitype *Nototarus papua* Darlington, 1968). The subtribe Cymindina includes the new Oriental genus *Ceylonitarus* (generitype *C. ceylonicus*, new species, with type locality vicinity of Mannar, Sri Lanka), the Megagean *Cymindis* Latreille, 1806, and the Afrotropical-western Palaeartic *Hystrihopus* Boheman, 1848. The genus *Cymindis* includes four subgenera (new rank): Oriental *Taridius* Chaudoir, 1875; Nearctic-Neotropical *Pinacodera* Schaum, 1857; Afrotropical-Oriental *Afrotarus* Jeannel, 1949; and Holarctic *Cymindis* sensu stricto. *Hystrihopus* includes four subgenera (new rank): Madagascan *Assadecma* Basilewsky, 1982; Afrotropical-Palaeartic *Pseudomasoreus* Desbrochers des Loges, 1904; Afrotropical *Hystrihopus* sensu stricto; and Afrotropical *Plagiopyga* Boheman, 1848. Transferred to the

subtribe *Calleidina* are the *Palaeartic- Old World Tropical- Australian* *Anomotarus* Chaudoir, 1875, and the *Australian* *Trigonothops* MacLeay, 1864. Transfer of *Anomotarus* renders the names *Calleidina* and *Anomotarina* synonyms; the latter name is junior. *Anomotarus* includes three subgenera: *Palaeartic- Old World Tropical- Australian* *Anomotarus* sensu stricto; *Australian* *Nototarus* Chaudoir, 1875, new rank (= *Lithostrotus* Blackburn, 1894, new synonymy); and *Afrotropical* *Dromiotes* Jeannel, 1949 (= *Cephalotarus* Mateu, 1973). *Trigonothops* includes five subgenera (new rank): *Trigonothops* sensu stricto; *Phloeocarabus* MacLeay, 1871; *Diabaticus* Bates, 1878; *Abaditicus* new subgenus (generic type *Diabaticus collaris* Blackburn, 1901); and *Speotarus* Moore, 1964. Transferred to the *Dromiina* is the *Afrotropical* (South African) genus *Metaxymorphus* Chaudoir, 1873, including as subgenera (new rank): *Metaxymorphus* sensu stricto; *Periphobus* Péringuey, 1896; and *Callidomorphus* Péringuey, 1896. Inclusion of the South African *Syndetus* Péringuey, 1896 (= *Coptoptera* Chaudoir, 1837) in the *Dromiina* is confirmed. The *Old World* *Agastus* Schmidt-Goebel, 1846 is transferred to the tribe *Zuphiini*. Also included in the *Dromiina* are the tribes *Lichnasthenini* and *Singilini*.

The *Madagascan* genera *Thysanotus* Chaudoir, 1837, *Antimerina* Alluaud, 1897, and *Madecassina* Jeannel, 1949 (formally tribe *Thysanotini*, subfamily *Calleiditae*) are placed in the subtribe *Pericalina*, with the name *Thysanotini* becoming thereby a junior synonym of the name *Pericalina*.

The name *Lachnaces sericeus* Bates, 1872 is changed to *Eucaerus* (*Lachnaces*) *sericeus*, thereby becoming a junior secondary homonym of *Eucaerus* (sensu stricto) *sericeus* Bates, 1871. *Eucaerus sericatus* is proposed as a name for the junior homonym.

The nominal species *Cymindis* (*Taridius*) *stevensi* (Andrewes, 1923) is expanded to include as subspecies *C. s. nilgirica* (Andrewes, 1935), *C. s. andrewesi* (van Emden, 1937), and *C. s. stevensi* sensu stricto. *Taridius niger* Andrewes, 1935 is transferred to subgenus *Afrotarus* Jeannel. New species of *Hystrichopus* (subgenus *Pseudomasoreus*) are described, based on material from the Union of South Africa: *H. (P.) reticulatus* (type locality— Cape Province, Clanwilliam District, Sederburg); *H. (P.) basilewskyi* (type locality— Cape Province, Swellendam Distr., Grootvaderbos); *H. (P.) thoracicus* (type locality— Grahamstown); and *H. (P.) mateui* (type locality Natal, Malvern). A new species of *Trigonothops* is described: *T. (Abaditicus) meyeri* (type locality— AUSTRALIA, Victoria, Nunniong Plateau, Woodhouse Creek).

## RÉSUMÉ

L'examen des caractères des adultes (en particulier des sclérites de l'ovipositeur), réalisé sur un échantillon limité de taxons jusqu'ici inclus dans la sous-tribu lébiienne des *Cymindina* (= tribus des *Cymindina* et des *Pseudomasoreini*, ou sous-famille des *Cyminditae* de certains auteurs), révèle que les tribus et sous-tribus suivantes y sont représentées: tribu des *Platynina*; tribu des *Lachnophorini*; tribu des *Lebiini*, sous-tribus des *Pericalina*, *Apenina*, *Cymindina*, *Calleidina* et *Dromiina*; et tribu des *Zuphiini*. Cette étude confirme en outre que le genre sud-africain *Anaromastus* Péringuey, 1896 (= *Euplynes* Schmidt-Goebel, 1846) est bien platynien. Les genres *Eucaerus* LeConte, 1853 et *Lachnaces* Bates, 1872, des régions tropicales et subtropicales du Nouveau Monde, sont inclus dans le complexe des *Eucaerus*, et transférés dans les *Lachnophorini*. *Eucaerus* et *Lachnaces* sont considérés comme des sous-genres congénériques (nouveau rang). Les genres néotropicaux *Asklepia* Liebke, 1938 et *Phaerodius* Liebke, 1951 sont également inclus dans le complexe *Eucaerus*. *Leptosarcus* Péringuey, 1896, du sud de l'Afrique, et *Selenoritus* Alluaud, 1917, des montagnes est-africaines [ce dernier étant considéré comme un sous-genre de *Thyreopterus* Dejean, 1831 (nouveau rang)], sont transférés dans la sous-tribu des *Pericalina*. Trois genres sont transférés dans la sous-tribu des *Apenina*: *Apenes* LeConte, 1851, du Nouveau Monde, comprenant les sous-genres *Apenes* sensu stricto (= *Malisus* Motschulsky, 1864), et *Sphalera* Chaudoir, 1875 (= *Didymochaeta* Chaudoir, 1875, synonyme nouveau); *Trymosternus* Chaudoir, 1873, de l'Eurasie; et *Cymindoidea* Castelnau, 1832, des tropiques de l'Ancien Monde. Ce dernier genre comprend les sous-genres *Cymindoides* (sensu



stricto, *Platyтарus Fairmaire, 1850 (nouveau rang), et Habutarus, nouveau genre (g  notype Nototarus papua Darlington, 1968). La sous-tribu des Cymindina comprend un nouveau genre de la r  gion orientale, Ceylonitarus (g  notype C. ceylonicus, nouvelle esp  ce, localit   du type situ  e dans les environs de Mannar, Sri Lanka), Cymindis Latrielle, 1806, r  parti en Am  rique du Nord, Eurasie et Afrique, et Hysteichopus Boheman, 1848, de l'Afrique tropicale et de la partie occidentale de l'Eurasie. Le genre Cymindis inclut quatre sous-genres (nouveau rang): Taridius Chaudoir, 1875, de la r  gion orientale; Pinacodera Schaum, 1857, des r  gions n  arctique et n  otropicale; Afrotarus Jeannel, 1949, des r  gions orientale et afrotropicale; et Cymindis sensu stricto de la r  gion holarctique. Hystrichopus comprend quatre sous-genres (nouveau rang): Assadecma Basilewsky, 1982, de Madagascar; Pseudomasoreus Desbrochers des Loges, 1904, des r  gions pal  arctique et afrotropicale; Hystrichopus sensu stricto, de la r  gion afrotropicale; et Plagiopyga Boheman, 1848, aussi de l'Afrique tropicale. Anomotarus Chaudoir, 1875, des r  gions pal  arctique et australienne ainsi que des tropiques de l'Ancien Monde, et Trignothops MacLeay, 1864, d'Australie, sont transf  r  s dans la sous-tribu des Calleidina. Calleidina et Anomotarina deviennent synonymes    la suite du transfert d'Anomotarus, Anomotarina   tant le plus r  cent des deux. Anomotarus sensu stricto, r  parti en Eirasia, dans les tropiques de l'Ancien Monde et dans la r  gion australienne; Nototarus Chaudoir, 1875, nouveau rang (= Lithostrotus Blackburn, 1894, nouveau synonyme), d'Australie; et Dromiotes Jeannel, 1949 (= Cephalotarus Mateu, 1973), de l'Afrique tropicale. Trigonothops comprend cinq sous-genres (nouveau rang): Trigonothops sensu stricto; Phloeocarabus MacLeay, 1871; Diabaticus Bates, 1878; Abaditicus nouveau genre (g  notype Diabaticus collaris Blackburn, 1901); et Speotarus Moore, 1964. Metaxymorphus Chaudoir, 1873, de l'Afrique tropicale (sud de l'Afrique) est transf  r   dans les Dromiina et inclut les sous-genres (nouveau rang) Metaxymorphus sensu stricto, Periphobus P  ringuey, 1896, et Callidomorphus P  ringuey, 1896. Cette   tude confirme en outre l'inclusion du genre sud-africain Syndetus P  ringuey, 1896 (= Coptoptera Chaudoir, 1837) dans les Dromiina. Agastus Schmidt-Goebel, 1846, de l'Ancien Monde, est transf  r   dans la tribu des Zuphiini. Les tribus des Lichnasthenini et des Singilini sont aussi incluses dans les Dromiina.*

Les genres malgaches *Thysanotus Chaudoir, 1837, Antimerina Alluaud, 1897, et Madecassina Jeannel, 1949 (formellement, de la tribu des Thysanotini, sous-famille des Calleidit  e)* sont inclus dans la sous-tribu des Pericalina, rendant ainsi le nom *Thysanotini* synonyme r  cent du nom *Pericalina*.

Le binome *Lachnaces sericeus Bates, 1872 est chang   en Eucaerus (Lachnaces) sericeus, et devient ainsi homonyme secondaire r  cent d'Eucaerus (sensu stricto) sericeus Bates, 1871. L'auteur propose Eucaerus sericatus comme remplacement de l'homonyme r  cent.*

La signification de l'esp  ce nominale *Cymindis (Taridius) stevensi Andrewes, 1923* est   largie piur inclure les sous-esp  ces *C. s. nilgirica (Andrewes, 1935), C. s. andrewesi van Emden, 1937, et C. s. stevensi sensu stricto. Taridius niger Andrewes, 1935 est transf  r   dans le sous-genre Afrotarus Jeannel. De nouvelles esp  ces d'Hystrichopus (sous-genre Pseudomasoreus) sont d  crites    partir de sp  cimens provenant de l'Union Sud-Africaine; ce sont: H. (P.) reticulatus (localit   du type: province du Cap, district de Clanwilliam, Sederburg); H. (P.) basilewskyi (localit   dy type: province du Cap, district de Swellendam, Grootvaderbos); H. (P.) thoracicus (localit   du type: Grahamstown; et H. (P.) mateui (localit   du type: Natal, Malvern). Une nouvelle esp  ce de Trigonothops est d  crite; il s'agit de T. (Abaditicus) meyeri (localit   du type: Australie, Victoria, plateau du Nunniong, Woodhouse Creek).*

## TABLE OF CONTENTS

Introduction . . . . .	96
Materials and Methods . . . . .	96
Materials . . . . .	96
Methods . . . . .	97
Structures used in Classification . . . . .	98
Classification . . . . .	98
Tribe Pterostichini, Subtribe Platynina . . . . .	99
Tribe Lachnophorini . . . . .	101
Tribe Lebiini . . . . .	108
Subtribe Pericalina . . . . .	116
Subtribe Apenina . . . . .	120
Subtribe Cymindina . . . . .	129
Subtribe Calleidina . . . . .	173
Subtribe Dromiina . . . . .	196
Tribe Zuphiini . . . . .	201
Concluding Remarks . . . . .	202

Acknowledgements .....	203
References .....	204
Index .....	213

## INTRODUCTION

During preparation of a revision of the species of the New World taxon *Pinacodera* Schaum, we wished to identify its sister group, and so undertook what was hoped to be a brief review of the genera that René Jeannel and other previous workers had included in the subtribe Cymindina. That outstanding Japanese student of Carabidae, Akinobu Habu (1967), showed that details of the ovipositor of adult lebiines were of substantial value in classification. We also knew that mandibles offered useful and previously unused character states.

Preliminary examination of these structures of adults of a few supposedly cymindine genera showed striking heterogeneity, so much so that it became evident that the cymindine assemblage was very likely to be unsatisfactory, at least from a phylogenetic viewpoint. This realization left us with three choices: to abandon the original goal, and to proceed with an analysis of *Pinacodera* without knowing the sister group; or to attempt to locate close relatives of *Pinacodera* and leave the rest of the cymindines for another time; or to attempt to sort out the group by assigning all genera to their proper subtribes, and at the same time, to identify the sister group of *Pinacodera*. We chose the last course, and this paper is the result.

At first, we thought that reclassification of the cymindine Lebiini would form the introductory part of a treatment of *Pinacodera*, but the introduction grew in volume and complexity, until it became obvious that inclusion of a detailed treatment of that genus would appear almost as an appendage. Therefore, revision of the species of *Pinacodera* will be published separately.

In the present paper, genera of the Cymindina of authors are briefly characterized on the basis of features of adults, and assigned to their proper groups. Several subtribes of Lebiini are characterized. Most genera are treated in cursory fashion, but for some, material was available for partial revision, and we took advantage of the opportunities thus offered.

This paper is not a revision of the higher classification of the Lebiini. It is more a collection of notes that ought to be useful for such a revision. Habu (1967) provided the basis for such a treatment, but structures of many more taxa must be examined in detail, to assess character systems thought to be of value, and to identify evolutionary trends.

## MATERIALS AND METHODS

### Materials

Several hundred lebiine adults were examined, representing described cymindine genera. A few taxa were represented in the Strickland Museum, University of Alberta (UASM), but most specimens were borrowed. Listed below, with abbreviations used in the text, are names and addresses of the lending institutions.

BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, England, SW7 5BD.

CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California U.S.A., 94118.

- CSIRO Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Black Mountain, Canberra City, ACT 2601, Australia
- IRSB Section d'Entomologie, Institut Royal des Sciences Naturelles du Belgique, Bruxelles 4, Rue Vautier 31, Belgium.
- MACT Musée Royal de l'Afrique Centrale, B- 1980, Tervuren, Belgique.
- MCZ Museum of Comparative Zoology, Harvard University Cambridge, Massachusetts, U.S.A. 02138.
- MNHP Entomologie, Muséum National d'Histoire Naturelle, Paris (Ve), France.
- SAMC South African Museum, P.O. Box 61, Cape Town, South Africa.
- USNM Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560.
- ZSIC Zoological Survey of India, 34 Chittaranjan Avenue, Calcutta, 700 012 India.

## Methods

Because of the nature of this study, most taxa were represented by few specimens. Therefore, no attempt was made to assess range of variation of character states studied, and few specimens of each taxon were dissected or measured. In general, however, characters used tend to be stable intraspecifically.

Taxonomic principles, criteria for ranking taxa, and general working methods were the same as those previously described (Ball, 1975 and 1978, and Allen and Ball, 1980), and are not repeated here. However, if we have erred in taxonomic judgement, it is in the direction of lumping rather than splitting, by emphasis of similarities that we felt are likely to represent close phylogenetic relationship, rather than emphasis of differences that, although they might be numerous, seem the sort of features that might change rapidly.

Genitalia and other small structures were preserved in glycerine, in microvials, pinned beneath the specimens from which they were removed.

Measurements made with a Wild M5 stereobinocular microscope, at 25X or 50X, are as follows, and are expressed in the text by these abbreviations:

- Hl- length of head, measured on left side, from base of left mandible to posterior margin of compound eye;
- Hw- maximum transverse distance across head, including eyes;
- Vwm- minimum transverse distance across vertex (used for specimens with markedly constricted head, posteriorly);
- Pl- length of pronotum, measured along mid-line, from base to apex;
- PwB- width of pronotum, at base;
- Pwm- maximum width of pronotum;
- MES l
- (and w)- length of metepisternum, measured along lateral margin; (width of metepisternum, measured along basal margin);
- El- length of longer elytron (if elytra of a single specimen were unequal) from basal ridge to apex.

Size was expressed in the text as the sum of Hl, Pl, and El, and referred to as Standardized Body Length, or SBL. Other measurements were used to form ratios which seemed to provide adequate diagnostic features for differentiation among members of some taxa.

For photographs of some structures, a Stereo Electron Microscope was used, Cambridge Model S150. Specimens were cleaned, using a sonicator, and were gold-coated.

### STRUCTURES USED IN CLASSIFICATION

All of the features used are standard for carabids, especially lebiines. Nonetheless, attention is drawn here to terms that have yet to be stabilized in the carabid literature for various structures.

For micro-units of surface sculpture bounded by lines of microsculpture, we use "sculpticell" (Allen and Ball, 1980: 486); for elytral stria, "interneur" (Erwin, 1974: 3-5). For abdominal sterna, Roman numerals are used, with first visible sternum being II, and the last one that is not normally retracted, VII.

The median lobe of the male genitalia is classified depending upon position of the apical orifice: anopic, if dorsal; catopic, if ventral (Jeannel, 1949: 878). For a discussion of the significance of catopy see Jeannel (1955: 82-86). The word "hemiotic" is used for median lobes in which the apical orifice is more lateral than it is dorsal or ventral (Ball and Shpeley, in press).

Sclerites of the ovipositor are named according to Tanner (1927), with modifications proposed by Noonan (1973), and Ball and Shpeley (in press). Thus, the terminal sclerite of the ovipositor is "stylomere 2", abbreviated S2. Terms used for surfaces are those proposed by Ball and Shpeley (in press), based on orientation of surfaces in the extended position.

### CLASSIFICATION

The cymindine genera of authors represent one subtribe of Pterostichini, the Lachnophorini, five subtribes of Lebiini, and the Zuphiini. As a guide to the text, we list by name these supraspecific taxa, as well as two that are new, and several not included in the Cymindina of authors, but related more or less directly to the general subject matter of this study.

#### Tribe PTEROSTICHINI

##### Subtribe PLATYNINA

*Anarmosta* Péringuey, 1896 (junior subjective synonym of *Euplynes* Schmidt-Göebel, 1846)

#### Tribe LACHNOPHORINI

*Eucaerus* LeConte, 1853

*Lachnaces* Bates, 1872

*Asklepia* Liebke, 1938

*Phaedrusium* Liebke, 1951

#### Tribe LEBIINI

##### Subtribe PERICALINA (including THYSANOTINI)

*Thysanotus* Chaudoir, 1837

*Antimerina* Alluaud, 1897

*Madecassina* Jeannel, 1949

*Selenoritus* Alluaud, 1917

*Thyreopterinus* Alluaud, 1932

*Thyreopterus* Dejean, 1831

*Leptosarcus* Péringuey, 1896

Subtribe APENINA

*Apenes* LeConte, 1851

*Malisus* Motschulsky, 1864

*Sphalera* Chaudoir, 1875

*Didymochaeta* Chaudoir, 1875

*Trymosternus* Chaudoir, 1873

*Cymindoidea* Castelanu, 1832

*Platytarus* Fairmaire, 1850

*Habutarus*, new subgenus

Subtribe CYMINDINA

*Ceylonitarus*, new genus

*Taridius* Chaudoir, 1875

*Pinacodera* Schaum, 1857

*Afrotarus* Jeannel, 1949

*Cymindis* Latreille, 1806

*Assadecma* Basilewsky, 1982

*Pseudomasoreus* Desbrochers des Loges, 1904

*Hystrichopus* Boheman, 1848

*Plagiopyga* Boheman, 1848

Subtribe CALLEIDINA

*Trigonothops* Macleay, 1864

*Phloeocarabus* Macleay, 1871

*Diabaticus* Bates, 1878

*Abaditicus*, new subgenus

*Speotarus* Moore, 1964

Subtribe DROMIINA (including LICHNASTHENINI and SINGILINI)

*Metaxymorphus* Chaudoir, 1873

*Periphobus* Péringuey, 1896

*Callidomorphus* Péringuey, 1896

*Syndetus* Péringuey, 1896 (junior subjective synonym of *Coptoptera* Chaudoir, 1837)

Tribe ZUPHIINI

*Agastus* Schmidt-Goebel, 1846

Details about these subtribes and genus-group taxa are provided below.

TRIBE PTEROSTICHINI, SUBTRIBE PLATYNINA

Genus *Euplynes* Schmidt-Goebel

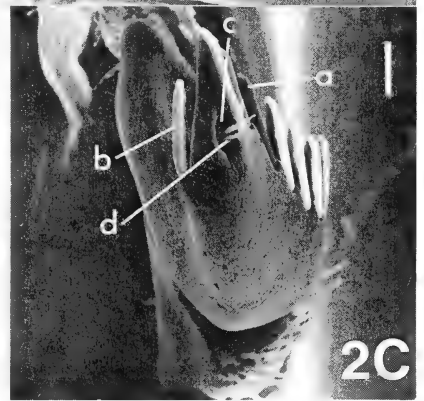
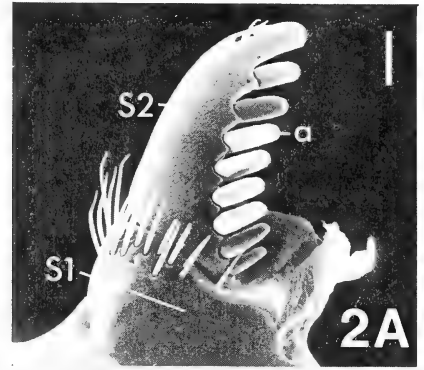
Figs. 1 and 2

*Euplynes* Schmidt-Goebel, 1846: 52. GENERITYPE: *Euplynes cyanipennis* Schmidt-Goebel, 1846: 52 (monotypy).– Burgeon, 1937: 397.– Jeannel, 1949: 611.– Mateu, 1974: 487-506.– Habu, 1978: 292.

*Euplenes* Darlington, 1952: 122.

*Xatis* Fairmaire, 1901: 125. GENERITYPE: *Xatis nigripes* Fairmaire, 1901: 125 (monotypy).– Jeannel, 1949: 611.– Habu, 1978: 294.

*Anarmosta* Péringuey, 1896: 221. GENERITYPE: *Anarmosta dispar* Péringuey, 1896: 222. (= *Euplynes callidoides* Chaudoir, 1878) (monotypy).– Mateu, 1974: 487.



Figs. 1 and 2. Photographs of Platynina, *Euplynes callidoides* Chaudoir (= *Anarmosta dispar* Péringuey).—Fig. 1: habitus, dorsal aspect (SBL = 9.79 mm). Fig. 2: SEM photograph of ovipositor, right stylomeres—A, lateral aspect; B, medial aspect; C, apico-ventral aspect. Scale bars = 50  $\mu$ m. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow peg; d, nematoid seta; S1, stylomere 1; S2, stylomere 2.

*Notes about types and synonymy.*— Although we have not seen type material, we have studied three specimens from the Péringuey collection (SAMC) from the type locality of Salisbury, and labelled as follows: male, Salisbury, Rhodesia, 17.1.11, J.A. O'Neill; female, Salisbury, 11.2.18; female, Salisbury, 3.11.1914, J. O'Neil. Additionally, each specimen bears: two determination labels (*Anarmosta dispar* Per.; and *Euplynes dispar* Pering. det. Ball, '80); and a museum label (SAMC). Mr. V. Whitehead, of the South African Museum, advised us that these were the only specimens available of this species in the Péringuey collection. The features of these specimens fit those provided in the original description. Fig. 1 illustrates the habitus of *E. callidoides* Chaudoir.

It seems difficult to believe that Péringuey would have placed a typical platynine among the Lebiini. However, there are some clues about how such an error could be made. First, his diagnosis of the "Lebiides" does not exclude specimens with approximately normal elytral apices ("...or very deeply sinuate behind..."). Second, in the key to genera of "Cymindidae" (included in the "Lebiides"), Péringuey gave the name "*Haplopeza*" following the singlet in which *Anarmosta* runs out, and the former name is not listed again. It seems likely that he originally regarded the specimen of *A. dispar* as belonging to *Haplopeza*, realizing at a later date (possibly when the manuscript was in press) that this was incorrect. *Haplopeza*, however, is a platynine. From this, we infer that *A. dispar*, although not a species of *Haplopeza*, is a platynine. We feel confident that the specimens labelled *Anarmosta dispar* Péringuey are indeed members of that nominal species. This is the same conclusion that Straneo (1943: 58) reached.

The above comments are not made to criticize Péringuey. Rather, they illustrate the difficulties that our predecessors had in distinguishing among lebiines and platynines, and especially some of the tropical members of these groups. As a further example of the problem, Bates (1883:158) suggested that *Euplynes* might be related to *Leptotrachelus*.

Figs. 2A-C illustrate the highly distinctive stylomere 2 of the ovipositor of *E. dispar*, with its dorso-lateral row of thick spines, and the well developed basal lobe. We think that it might be a generic character state for *Euplynes*. Habu's illustrations (1978: 293-295, Figs. 590-592a) of Oriental- eastern Palaearctic females are about the same as our Fig. 2. Jeannel (1949: 611) suggests that the African genus *Haplopeza* Boheman is related to *Euplynes*.

Mateu (1974) revised the African species of *Euplynes*.

### Tribe LACHNOPHORINI

To this tribe, four genus-group taxa are assigned: *Eucaerus* LeConte, *Lachnaces* Bates, *Asklepiea* Liebke, and *Phaedrusium* Liebke. We have seen representatives of only the first two groups. T. L. Erwin (personal communication) suggested that the latter two groups should be included, also. Figures provided by Reichardt (1974: 178, Figs. 1, and 3-7) confirm that *Asklepiea* is indeed like *Eucaerus*, and the original description of *Phaedrusium* (Liebke, 1951: 240-241) includes mention of character states that are *Eucaerus*- like.

The marked similarity of adults of *Lachnaces* and *Eucaerus* in several features is taken as evidence of very close relationship of these taxa. Therefore, we combine them as subgenera of a single genus. We believe that re-examination of specimens of *Asklepiea* and *Phaedrusium* will show that these groups should be included in *Eucaerus*, as well.

Reichardt (1974: 178) transferred *Asklepiea* Liebke from the Colliurini to the Lachnophorini, and *Phaedrusium* was compared with lachnophorines (*Lachnophorus* and

*Calybe* by Liebke (1951: 241), though he included the genus in the Lebiini. Bates (1871: 77) noted both lachnophorine and lebiine affinities of *Eucaerus*. Horn (1881: 155) commented about the lachnophorine affinities of *Eucaerus*, referring to it as "an osculant form" between that group and the Lebiini. He decided, nonetheless, that *Eucaerus* was a lebiine, a view that was accepted by subsequent cataloguers and American workers (see Ball, 1960: 162, and Reichardt, 1977: 444).

Terry L. Erwin (personal communication) suggested that this complex belonged in the Lachnophorini, and we place it there on the basis of: terminal palpomeres with acuminate tips (Figs. 10 and 12); mandibles of same form (details provided in description of *Eucaerus*); elytral apices subtruncate; wings with oblongum cell reduced (stalked), wedge cell absent; stylomere 1 of ovipositor with terminal row of setae, stylomere 2 of plesiotypic form and setation (Figs. 17 and 18). Form of palpomeres is autapotypic. Details of wing venation are also apotypic, but could have been independently acquired by reduction. Mandibles are probably a mixture of symplesiotypic and autapotypic features. We cannot sort out the details at this time. All antennomeres of *Eucaerus* (*sensu stricto*) and *Asklepia* adults have a vestiture of short setae, like antennomeres 4-11. Antennomeres 1-3 of *Phaedrusium* adults and antennomere 1 of subgenus *Lachnaces* adults are without such vestiture, contrasting with antennomeres 4-11.

According to Reichardt (1977: 413), the Lachnophorini (excluding *Anchonoderus* Reiche) is "A weakly characterized tribe of still uncertain position and constitution". He provided an account of the taxonomic history of the group (1977: 406 and 413), which has been treated as an independent tribe near the Perigonini (with or without *Anchonoderus*), or as a subtribe of the Pterostichini. Liebherr (MS) presents evidence based on structural features of larvae and adults, showing clear lebiomorph affinities of lachnophorines, and this is our basis for ranking this group (including *Anchonoderus*) as a tribe apart from the Pterostichini, and placing it in the lebiomorph assemblage. Further work might require including in a single tribe the lachnophorines and lebiines, but this possibility remains to be investigated.

*Geographical distribution.*— This complex is confined to the tropics and warm temperate areas of the New World: all four genera are known from South America, but only *Eucaerus* ranges north to Middle America and to southeastern United States.

*Description of the Eucaerus complex.*— The following describes range of variation of selected features useful in recognizing lachnophorine taxa, and for determining their relationships.

*Color.* Various, from somber to pale; dorsum all black to combinations of rufous and testaceous, elytra spotted or not; legs and palpi testaceous; antennae uniformly testaceous, or tricolored, antennomeres 1-3 rufous or piceous, 4-6 black, and 7-11 white.

*Microsculpture.* Various, but generally transverse: some members of *Eucaerus* with dorsum of head and/or pronotum with isodiametric meshes and sculpticells convex, surface thus beaded.

*Luster.* Generally iridescent, or dorsum of head and pronotum dull.

*Macrosculpture.* Dorsum generally smooth, without constant depressions or swellings, but frontal impressions with transverse rugulae; ventral surface rather coarsely but sparsely punctate.

*Vestiture.* Dorsal surface generally glabrous; all antennomeres setose; or antennomeres 1 or antennomeres 1-3 glabrous except for normal preapical setae; terminal palpomeres densely setose; maxillary palpomere 3 densely setose, palpomere 2 sparsely setose; ventral surface sparsely setose.

*Fixed setae.* Average for lachnophorine adults: labrum with six long apical setae; head and pronotum with two pairs; elytron with three setae on interval 3, or in *Asklepia strandi* adults, with two rows of setae on disc; umbilical series of about 10-12 setigerous punctures laterally, broadly interrupted medially, penultimate lateral seta in straight line with antepenultimate and ultimate setae.

*Head.* Clypeus transverse, anterior margin truncate. Frontal impressions broad and shallow or deep and linear. Sub-antennal ridge average. Eyes orbicular, convex, prominent. Antennae average for lachnophorine adults: filiform, flagellar antennomeres sub-cylindrical distinctly longer than wide; antennomere 2 short, 3 longer than 4.



Mouthparts. Labrum with anterior margin truncate. Left and right mandibles about same in overall shape. Scrobes less than 0.50 total length of mandibles, ventral edge of scrobe curved upward. Left mandible (Figs. 3A, C, 4A, C, 5A, C) with terebral ridge distinct, extended more than half length of terebra; terebral tooth absent; retinacular ridge cutting edge; retinacular tooth prominent, cleft, ventral ridge well developed; premolar tooth blunt, small, set off from posterior part of retinacular ridge by indentation; ventral premolar ridge not developed. Right mandible (Figs. 3B, D, 4B, D, 5B, D) cutting edge terebral ridge anteriorly, retinacular ridge posteriorly; terebral tooth blunt; retinacular ridge well developed; anterior retinacular tooth prominent in *Eucaerus*, small in *Asklepia*; (Reichardt, 1974: Fig.6); premolar tooth blunt, small, continuous with retinacular ridge; ventral premolar ridge indistinct. Ventral grooves long, setose, extended more than 0.5 length of mandibles. Maxilla (Figs. 6-7) with sclerites generally elongate; lacinia with long setae on dorsal surface; galeomere 2 distinctly shorter than 1; palpomere 4 slightly swollen, subulate apically. Labium with mentum bisetose, median tooth developed (some members of *Lachnaces*), or not, or very slightly developed; lateral lobes pointed apically; epilobes expanded apically; glossal sclerite narrow, bisetose, keeled ventrally; paraglossae membranous, glabrous either shorter (Fig. 10) or longer (Fig. 12) than glossal sclerite; palpus with palpomeres 1 and 2 slender, 3 swollen, subulate apically.

Thorax. Pronotum various: subcordate (Fig 13) to pronouncedly transverse; base lobed or not; anterior angles broadly rounded, posterior angles sharp or rounded; disc slightly convex, median longitudinal impression sharp, well developed; anterior and posterior lateral impressions well developed. Metepisternum distinctly longer than wide.

Elytra. Average in form; humeri broadly rounded; basal ridge marginal, prominent, extended to scutellum; apical margin obliquely subtruncate. Interneurs average or effaced, impunctate.

Wings. Well developed; wedge cell absent, oblongum cell stalked, well developed. Venation otherwise normal for carabids.

Legs. Generally average for Lachnophorini. Tarsomere 4 with apical margin sub-truncate, tarsomere 5 with row of ventro-lateral setae, each side. Male anterior tarsus ventrally (Figs. 14-16) with reduced adhesive vestiture, on tarsomeres 2 and 3; present or not on tarsomere 1; tarsomere 4 with pair of flattened, expanded sense organs apicoventrally (Fig.14B).

Abdominal sterna. Average for Carabidae, in form; surface generally setose, or glabrous.

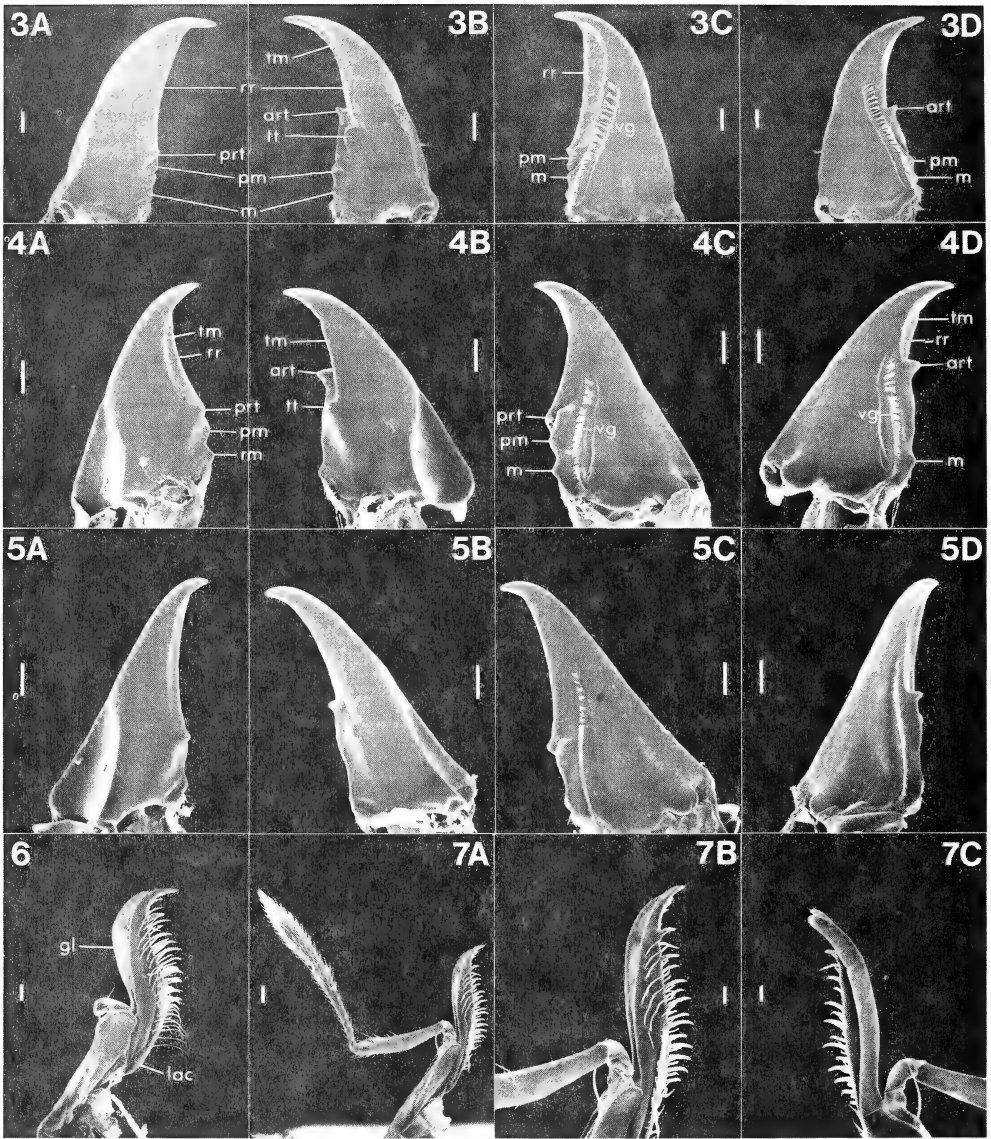
Male genitalia. Median lobe relatively broad in cross section, dorsal surface mostly membranous; apical orifice dorsal. Internal sac with microtrichial fields only, or with latter and varied number and groups of spines. Parameres average for Lachnophorini.

Ovipositor and associated abdominal sclerites. Tergum VIII completely sclerotized basally, not divided into two parts by median membranous area; apodemes with apices curved laterad. Sternum VIII extensively unsclerotized medially. Tergum X transverse, narrow. Valvifers average. Stylomeres 1 and 2 subequal in length, stylomere 1 with row of setae apically, stylomere 2 (Figs.17A, 18A) falcate, blade slender, with preapical sensory furrow and long nematoid setae on ventral surface, with two or three long spines on dorso-lateral margin, one on dorso-medial margin; row of sensory pits on lateral and ventral surfaces.

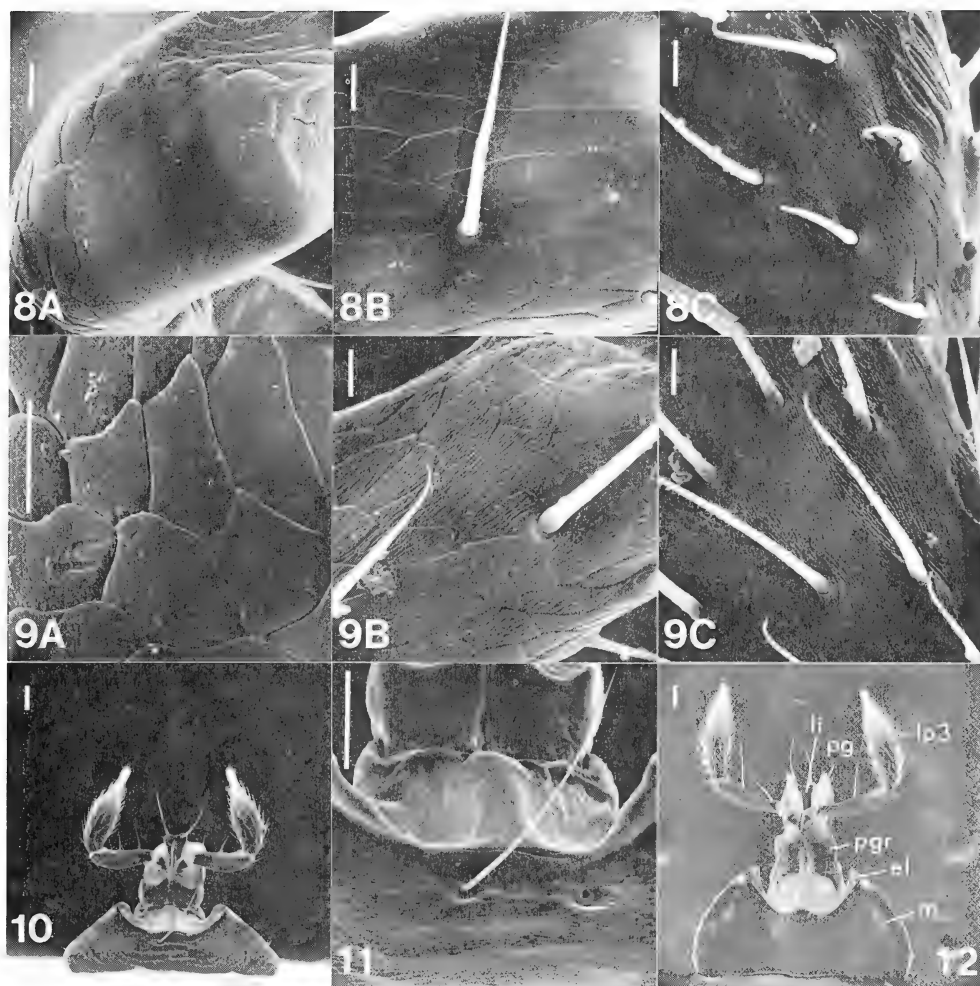
## Key to Genera of the Eucaerine Complex

- 1 (0) Pronotum with base truncate, not lobed medially. Disc of elytron with two rows of setigerous punctures; interneurs effaced, intervals flat; bicolored; microsculpture not evident at ordinary magnifications (to 50X) ..... *Asklepia* Liebke.
- 1' Pronotum with base lobed medially (Fig. 13). Elytral disc with single row of setigerous punctures (on interval 3); interneurs effaced or evident; concolorous or bicolored; microsculpture not evident, or meshes transverse ..... 2.
- 2 (1') Antennomeres 1-3 without vestiture of short setae, glabrous except for few, normal (long) preapical setae. Male anterior tarsomeres ventrally without adhesive vestiture ..... *Phaedrusium* Liebke.
- 2' Antennomeres 1-3 (or 2-3) with vestiture of short setae, like antennomeres 4-11. Male anterior tarsomeres 2 and 3, or 2-4 ventrally with adhesive vestiture (Figs. 14A, 15, and 16) ..... *Eucaerus* LeConte, p. 107

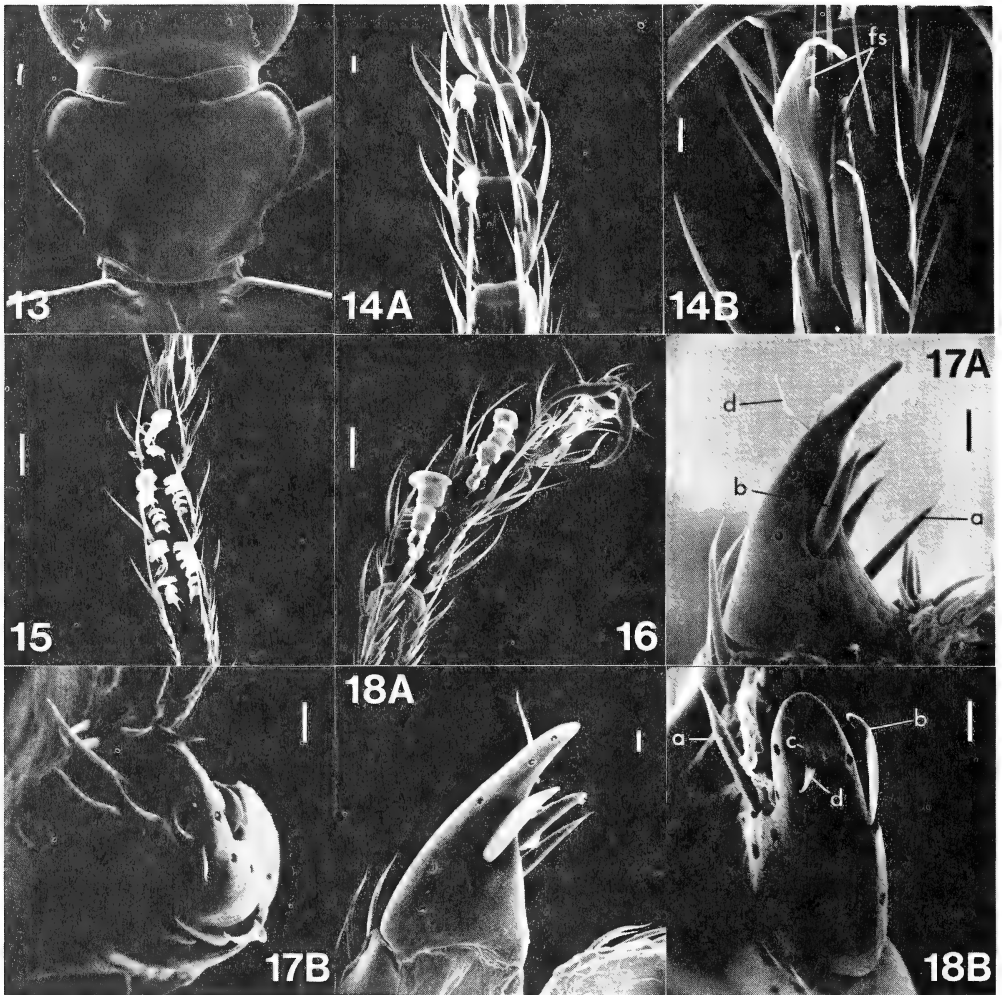
The genus *Asklepia* includes the single species *A. strandi* Liebke, 1938. *Phaedrusium* Liebke, 1951 includes *P. suturalis* Liebke, 1951 (generitype), and *P. titschacki* Liebke, 1951. We have nothing further to add about these genera.



Figs. 3–7. SEM photographs of structures of Lachnophorini.— Figs. 3–5: mandibles, A and C, left, dorsal and ventral aspects, respectively, B and D, right, dorsal and ventral aspects, respectively, of: 3, *Lachnophorus guttulatus* Bates; 4, *Eucaerus* (sensu stricto) species; 5, *E. (Lachnaces) olisthopoides* (Bates). Figs. 6–7: right maxilla of—6, *Eucaerus* (sensu stricto) species, ventral aspect; 7, *E. (Lachnaces) olisthopoides* (Bates), A, entire structure, ventral aspect, B, lacinia and galea, ventral aspect, C, galea and lacinia, dorsal aspect. Scale bars = 50  $\mu$ m. Legend, mandibles: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; vg, ventral groove. Legend, maxilla: gl, galea; lac, lacinia



Figs. 8–12. SEM photographs of Lachnophorini.—Structures of the labium. Figs. 8 and 9, palpomeres, microsculpture, A, palpomere 1, B, palpomere 2, and C, palpomere 3, of: 8, *Eucaerus (sensu stricto)* species; 9, *E. (Lachnaces) olishopoides* (Bates). Scale bars = 5  $\mu$ m, Fig. 10: labium, ventral aspect, of *Eucaerus (sensu stricto)* species. Fig. 11: mentum and palpigers, ventral aspect, of *Eucaerus (sensu stricto)* species. Fig. 12: labium, ventral aspect, of *E. (Lachnaces) olishopoides* (Bates). Scale bars = 50  $\mu$ m. Legend: el, epilobe; li, glossal (or ligular) sclerite; lp3, labial palpomere 3; m, mentum; pg, paraglossae; pgr, palpiger.



Figs. 13–18. SEM photographs of structures of Lachnophorini.—Fig. 13: bases of head and elytra, and pronotum, dorsal aspect, of *Eucaerus (sensu stricto) hilaris* Bates. Figs. 14–16, front tarsomeres of males, ventral aspect, showing adhesive vestiture: 14, *Eucaerus (sensu stricto) hilaris* Bates, A—tarsomeres 1–4, B—tarsomere 4; 15, *Eucaerus (sensu stricto)* species, tarsomeres 1–4; 16 *E. (Lachnaces) olisthopoides* (Bates), tarsomeres 1–5. Figs. 17–18: ovipositor, left stylomeres, A—medial aspect, B—apico-ventral aspect, of: 17, *Eucaerus (sensu stricto)* species; 18, *E. (Lachnaces) olisthopoides*. Scale bars, Figs. 13, 15, 16 = 50  $\mu$ m; Figs. 14, 17, 18 = 10  $\mu$ m. Legend, for tarsi: fs—foliose seta. Legend, for stylomeres: a, lateral ensiform seta; b, medial ensiform seta; c, furrow pegs; d, nematoid seta.

*Eucaerus* LeConte

Figs. 4-18

*Eucaerus* LeConte, 1853: 386. GENERITYPE: *E. varicornis* LeConte, 1853 (monotypy).— 1862: 22.— Chaudoir, 1871: 285.— Horn, 1881: 157, 159.— 1882: 158.— LeConte and Horn, 1883: 45.— Csiki, 1932: 1497.— Leng, 1920: 67.— Blackwelder, 1944: 63.— Ball, 1960: 162.— Erwin *et al*, 1977: 4: 60.

*Lachnaces* Bates, 1872: 201. GENERITYPE: *L. sericeus* Bates, 1872: 201 (here designated). Csiki, 1932: 1497.— Blackwelder, 1944: 63. NEW SYNONYMY.

*Note about nomenclature.*— The name *Lachnaces sericeus*, 1872 becomes *Eucaerus sericeus* by virtue of combining *Eucaerus* and *Lachnaces*. However, in 1871, Bates had already proposed the name *E. sericeus* for another species. Thus, the Bates name of 1872 becomes a junior secondary homonym. For the species to which that name applied, we propose *E. sericatus*, new name.

*Classification.*— The species of *Eucaerus* are arranged in two subgenera and two species groups, as indicated in the following key.

**Key to Subgenera and Species Groups of *Eucaerus* LeConte**

- 1 (0) Antennomere 1 without vestiture of short setae. Pronotum subquadrate, sides rounded, not sinuate; disc smooth, without pair of shallow depressions; surface iridescent, microsculpture meshes transverse, in form of diffraction grating. Elytron with interneurs average, intervals convex. Maxillary palpomere 3 longer than antennal scape. Labium with mentum as long as wide; paraglossa (Fig. 12) narrow apically, longer than glossal sclerite. Male front tarsomere 1 without adhesive vestiture ventrally, tarsomeres 2 and 3 with single row, only (Fig. 16). Median lobe of male genitalia with apical portion very short and broad; internal sac without spines ..... subgenus *Lachnaces* Bates.
- 1' Antennomere 1 with vestiture. Pronotum (Fig. 13) cordate, sides markedly sinuate posteriorly, posterior angles sharp; disc with pair of paramedian shallow depressions; pronotum with surface iridescent, microsculpture meshes grated, not visible at 50X, or surface dull, meshes isodiametric, microlines visible at 50X. Elytron with interneurs average or effaced, intervals convex or flat. Maxillary palpomere 3 shorter than antennal scape. Labium (Fig. 10) with mentum wider than long; paraglossa broad apically, shorter than glossal sclerite. Male front tarsomere 1 with or without adhesive vestiture; tarsomeres 2 and 3 with vestiture uniseriate (Fig. 14A) or biseriate (Fig. 15). Median lobe of male genitalia with apical portion very short, or longer; internal sac with or without spines ..... *Eucaerus (sensu stricto)* ..... 2
- 2 (1') Pronotum with sides narrow, proepisternum visible from dorsal aspect. Elytra bicolored. Head and pronotum smooth, microlines absent. Elytra with interneurs impressed or not, meshes transverse, surface iridescent, or microlines obsolete, surface shining. Male front tarsomere 1 without adhesive vestiture, tarsomere 2 and 3 with vestiture uniseriate. Median lobe with apical portion short ..... *E. hilaris* Group.
- 2' Pronotum (Fig. 13) with sides average, proepisternum not visible from dorsal aspect. Elytra concolorous. Head and pronotum with surface dull, microsculpture meshes isodiametric; elytra with surface iridescent, microlines in form of diffraction grating. Elytra with interneurs normally developed. Male

front tarsomeres 1-3 with biseriate adhesive vestiture. Median lobe with apical portion larger . . . . . *E. varicornis* Group.

*List of species.*— The senior author has studied representatives of all described species of *Eucaerus*. Names are listed here, and the species are assigned to their respective groups.

Subgenus *Eucaerus*

*E. varicornis* Group

*E. sulcatus* Bates

*E. striatus* Bates

*E. sericeus* Bates

*E. opacicollis* Bates

*E. insularis* Darlington

*E. haitianus* Darlington

(additionally, three undescribed species from Mexico).

*E. hilaris* Group

*E. geminatus* Bates

*E. hilaris* Bates

*E. lebioides* Bates

*E. pulchripennis* Bates

Subgenus *Lachnaces* Bates

*E. sericatus*, new name (= *E. sericeus* Bates, 1872, not 1871).

*E. badestrinus* Bates

*E. olisthopoides* Bates

*Notes about habitat.*— Members of this genus live in leaf litter, in swamp forest, or in flood zones along tropical rivers. Adults of the *E. hilaris* Group are in litter in areas with more light, close to river edges, whereas adults of the *E. varicornis* Group and *Lachnaces* are in more densely shaded places. On the Rio Negro, in northern Brazil, adults of the latter two groups are microsympatric.

*Geographical distribution.*— Species of subgenus *Lachnaces* and of the *E. hilaris* Group are known only from the Amazon Basin, in Brazil. Range of the *E. varicornis* Group extends from the Amazon Basin northward to southeastern United States, and eastward to the Greater Antilles. However, no species are shared between South America and areas further north, nor between the West Indies and the adjoining continents.

## Tribe LEBIINI

As background for more detailed consideration of cymindines, we need to comment about the tribe Lebiini, which includes the subtribe Cymindina. Collectively, lebiine adults are strikingly divergent in form, color, and in more detailed external features, making it difficult to provide a simple diagnosis for recognition of the tribe. Some adults (cymindines) look much like platynines, others (*Nemotarsus* members) have the long pectinate tibial spurs of masoreines, others (some *Lebia* members) are hardly different from pentagonicines in form and color, and still others (members of *Agra*) are colliurine- like. Internal features and mouthparts offer a similar range of attributes. While it seems unlikely that the Lebiini is a polyphyletic taxon, it could very well be paraphyletic. It is polythetic, for most character states used for recognition of the group are not shared by all member taxa, and those states that seem to be almost universal (biperforate anterior coxal cavities, two pairs of supraorbital setae, for example) are shared with members of non-lebiine taxa.

We are not, however, prepared to pursue this subject further. These comments are words of caution for those who use the following list of features for identification of adults, or those who wish to pursue phylogenetic studies of carabids.

*Recognition.*— Most lebiine adults exhibit most of these character states: apical margins of elytra truncate or subtruncate; tergum VIII more or less extensively membranous medially, laterally exposed, each side posteriorly with a projection that bears the openings of ducts of defensive glands; head with two pairs of supraorbital setigerous punctures; tibial spurs of middle and posterior legs of equal length, smooth, not serrate (if unequal and serrate, head sharply constricted posteriorly); terminal palpomeres more or less pubescent, apical margins subtruncate or truncate (not swollen medially and tapered to narrow apex); antennomeres 4-11 setose; front tarsomeres 1-3 of males with biseriate adhesive vestiture; anterior coxal cavities biperforate; abdomen with sternum X principally membranous; median lobe of male genitalia with dorsal surface extensively sclerotized, membranous area relatively small; right paramere smaller than left paramere; ovipositor with stylomere 1 setose or spinose.

Some pericaline and gallerucoid calleidine adults have virtually complete elytra, with apices extended to the apex of tergum VII. However, pericalines are recognized by a combination of well developed suborbital setae, displaced penultimate umbilical setigerous puncture, and long, slender labrum. Gallerucoid calleidines are chrysomelid-like in appearance, with well developed suborbital setae on the head.

*Notes about classification.*— The tribe Lebiini, as generally accepted by carabid specialists (for example, LeConte and Horn (1883), Sloane (1923), Andrewes (1929), Ball (1960), Lindroth (1969), and Erwin (1979)) was assembled by Horn (1881: 154), who combined the Lebiides and Pericalides of Lacordaire (1854), but excluded the genera *Mormolyce* Hagenbach and *Agra* Fabricius. Subsequently, these genera were returned to the Lebiini (*Mormolyce*, by Ball, 1975: 147, and *Agra*, by Erwin, 1978: 263). Erwin (1979: 590) also returned the eucheiline genera *Eucheila* Dejean and *Inna* Putzeys to the Lebiini.

Grouping the numerous lebiine genera has been a problem since it was first attempted by Lacordaire (1854: 102). In addition to the Pericalides, he recognized three basic forms centering on *Cymindis* Latreille, *Dromius* Bonelli, and *Lebia* Latreille. Lacordaire wrote that he was unable to find diagnostic characters for such groups.

Chaudoir gave tribal ranking to these groups, as well as to several others, based on slight differences in structure of the labium, as well as on other features. Horn (1881) undertook a detailed study of maxillae and labia of carabids, and one of his conclusions was that the differences among lebiine tribes were too slight and inconstant to be valid as taxonomic characters at the tribal level. Horn's lead was followed by European workers of the late 19th and early 20th centuries. For example, Csiki (1932: 1305-1500) included in the Lebiini most of the groups that Horn had included. He recognized seven subtribes, four of which were groups proposed by Lacordaire: Lebi, Catascopei (equivalent to Pericalides), Dromii, and Cymindina. Three other subtribes were established for genera included by Lacordaire in one or the other of his groups of Lebiides: Physoderi, Lebidii, and Callidi. Nemotarsines, agrines, and masoreines were excluded, each being assigned to a tribe of its own.

Jeannel (1949: 876-1039) used a system similar to that of Lacordaire, for organizing the lebiine fauna of Madagascar, but he excluded nemotarsines and masoreines. He recognized three families (Lebiidae, Thyreopteridae, and Lionychidae), the second including many of the genera that Lacordaire included in the Pericalides. Jeannel included physoderines and lebidines in the Lebiidae. Genera of Lebiidae were arranged in five subfamilies: Cyminditae, Lebiitae (including also physoderines), Coptoderitae, Calleiditae (including Lebidii), and Dromiitae. Genera of Thyreopteridae were arranged in two subfamilies: Thyreopteritae and Pericalitae. Lionychidae, a new family, included four genera regarded as dromiines by most



authors.

Jedlička (1963: 295-464) recognized the same seven subtribes into which Csiki arranged the genera of Lebiini.

Habu (1967: 60) recognized eight subtribes: Cymindina, Catascopina, Pericalina, Anomotarina, Calleidina, Lebiina, Demetriina, and Dromiina. The Cymindina and Lebiina are each about the same as proposed by Csiki; catascopines and pericalines are the equivalent of Catascopi; demetriines (proposed first by Bates (1886: 207)) and dromiines are the equivalent of Dromii; and calleidines (including Lebiidina and Physoderina) and anomotarines (new subtribe) are the equivalent of Callidi.

It is evident that central to these more or less divergent arrangements is the system proposed by Lacordaire, with various assemblages of his four basic groups (three of Lebiides plus Pericalides) shifted about on the basis of detailed study and weighting of various character systems. Authors previous to Habu relied principally on details of structure of: labium (particularly of the ligula); pronotum; and tarsi, particularly form of tarsomere 4 and pectination of the claws. Habu used these features, and also form of mandibles and details of structure and armature of the ovipositor sclerites.

Although Habu's treatment is restricted to the fauna of Japan and adjacent islands, most of the major groups of lebiines are represented there. His illustrations of structures are profuse, well-chosen, and well executed, his descriptions are detailed and accurate, and he has exhibited a good sense of proportion in ranking. It seems to us that Habu has provided a firm basis for resolving the long-standing problem of recognition of natural (i.e., phylogenetically valid) groups of lebiines.

To work out a phylogenetically valid classification, it is necessary to reconstruct the phylogeny of the Lebiini. Clues are provided by association of many groups of lebiines with vegetation, and at least some character states of adults (particularly those of the tarsi) seem to be associated with life above the surface of the ground (Erwin, 1979: 552). Which way has evolution of lebiines proceeded: from occupation of terrestrial to arboreal habitats; or from arboreal to terrestrial; or from terrestrial to arboreal and back to terrestrial? The same sorts of questions are applicable to arboreal habitats. Some lebiines live principally on tree trunks, others hunt on small branches and twigs, still others on leaf surfaces (Erwin, 1979: 559-560, Table 1). What has been the direction of evolution within arboreal habitats?

If these questions could be answered for all comparisons of taxa thought to be related, it would be possible to work out a classification consonant with direction of habitat change. Probably the arboreal zone has been invaded by terrestrial-based ancestors (Erwin, 1979: 509, Fig. 13), but it also seems likely that some ancestral stocks have given rise to terrestrial inhabitants, as well. Movements in both directions may have taken place several times.

Structure of the ovipositor may be associated with different modes of egg-laying, and if these modes were known they might offer another basis for inferring evolutionary sequences. Mode of oviposition is known for some terrestrial calleidines: females of *Tecnophilus* and *Philophuga* climb on low plants, carrying on the stylomeres of the ovipositor a small ball of mud. An egg is laid in the mud ball, and the latter is suspended from a twig by a silken thread produced by the female (Larson, 1969: 64).

Females of most groups of carabids are believed to oviposit in the ground, in chambers scooped out by the ovipositor. Compared to the latter, calleidines seem to be apotypic in oviposition. The ovipositor of *Tecnophilus* and many other calleidines is characterized by absence of ensiform setae from stylomere 2 and narrow form, whereas females of



ground-ovipositing carabids have broader second stylomeres and ensiform setae.

Erwin (1982: 40), referring to the remarkable telescopic ovipositor that characterizes females of the genus *Agra*, inferred that such structures are used to lay eggs "deep in existing burrows in wood or in other deep fissures". Stylomeres of *Agra* females also seem apotypic in their elongate form and reduced number of spine-like ensiform setae.

Among lebiines, pericalines (most taxa are arboreal) and apenines (all known taxa are terrestrial) have the more plesiotypic form of ovipositor. However, almost nothing is known about where eggs are laid or how they are laid by members of these groups. (An exception is the genus *Eurycoleus*, females of one species of which lay eggs on the surfaces of wood, near endomychid pupae which the developing *Eurycoleus* larvae eat [Erwin and Erwin, 1976]). We are satisfied that evidence from structure of the ovipositor offers sufficient grounds to infer that apenines and pericalines are relatively primitive lebiines, that cymindines, with moderately modified ovipositors, occupy an evolutionarily intermediate position, and that the other subtribes whose females have highly modified ovipositors, represent more highly evolved groups. Details of relationships among genera and subtribes remain to be worked out.

In lieu of a definitive treatment of classification of the Lebiini, we offer a key to the subtribes, based on features of adults.

### Key to Subtribes of Lebiini

- 1 (0) Head ventrally with at least one pair of suborbital setigerous punctures . . . . . 2.
- 1' Head ventrally without suborbital setigerous punctures . . . . . 4.
- 2 (1) Labrum narrow, as long or longer than wide. Penultimate setigerous puncture of umbilical series of elytron displaced laterally (as in Fig. 27B) . . . . . Subtribe Pericalina, p. 116
- 2' Labrum normal, wider than long. Penultimate setigerous punctures of elytra not displaced laterally . . . . . 3.
- 3 (2') Elytron smooth, without striae. Pronotum with sides curved, widest near base, narrowed evenly anteriorly, apical margin much narrower than basal margin. Head sharply constricted posteriorly, pedunculate. Stylomere 2 of ovipositor with broad apex, without ensiform setae . . . . . gallerucoid Calleidina.<sup>1</sup>
- 3' Elytron striate. Pronotum with sides sinuate posteriorly, widest at or anterior to middle. Head gradually constricted posteriorly. Stylomere 2 of ovipositor with narrowed apex, ensiform setae two, one dorsal, one ventral . . . . . genus *Euproctinus* Leng and Mutchler, 1927.<sup>2</sup> p.
- 4 (1') Penultimate setigerous puncture of elytron displaced laterally. Stylomere 2 of ovipositor with ensiform setae, and stylomere 1 with prominent ventral projection extended beyond base of stylomere 2 (Figs. 38 and 39) . . . . .

<sup>1</sup>Adults of *Lebidia* Morawitz and *Gallerucidia* Chaudoir (Lebidii or Gallerucidiini, of authors) key out here although in all other respects they seem to be calleidine.

<sup>2</sup>This Neotropical and southern Nearctic genus seems to be of uncertain position. It has been included with calleidines, based on general appearance and structure of tarsi, but Larson (1969: 23) suggested *Euproctinus* should be placed in a subtribe of its own.

- ..... Subtribe Apenina, p. 120
- 4' Penultimate setigerous puncture of elytron not displaced laterally, thus in line with rest of series, or displaced toward stria 8. Stylomere 1 of ovipositor without projection; stylomere 2 with (Fig. 62A) or without (Fig. 96B) ensiform setae . 5.
- 5 (4') Posterior tibial spurs markedly unequal, margins serrate, inner spur almost as long as tarsomere 1. Head sharply constricted posteriorly, pedunculate ..... Subtribe Nemotarsina.
- 5' Posterior tibial spurs subequal, margins smooth, not markedly serrate. Head sharply constricted or not ..... 6.
- 6 (5') Mandible widened near base, scrobe wide, lateral margins markedly rounded . 7.
- 6' Mandible not conspicuously widened basally, scrobe narrowed, lateral margins not markedly rounded ..... 8.
- 7 (6) Head markedly narrowed and prolonged behind eyes. Pronotum longer than wide, markedly narrowed anteriorly, without lateral flange. Ovipositor strikingly telescopic, stylomere 2 elongate ..... Subtribe Agrina.
- 7' Head average, not markedly prolonged behind eyes (Fig. 101). Pronotum wider than long, or as wide as long, not markedly narrowed anteriorly, basal and apical margins subequal in width, with lateral flange. Ovipositor not strikingly telescopic, stylomere 2 not especially lengthened ..... Subtribe Calleidina, p. 173
- 8 (6') Tarsomeres broad, tarsomere 4 with apex subtruncate, not bilobed. Female with stylomere 2 with one or two ensiform setae (Fig. 55A) ..... Subtribe Cymindina, p. 129
- 8' Tarsomeres broad, with tarsomere 4 bilobed, OR tarsomeres slender and tarsomere 4 with apical margin sub-truncate. Stylomere 2 of ovipositor without ensiform setae ..... 9.
- 9 (8') Tarsomeres slender, tarsomere 4 with apical margin sub-truncate. Stylomere 2 of ovipositor glabrous or setose apically ..... Subtribe Dromiina<sup>3</sup> p. 196
- 9' Tarsomeres stout, dilated, tarsomere 4 bilobed. Ovipositor with stylomere 2 glabrous ..... 10.
- 10 (9') Tarsomere 4 with lobes almost half length of tarsomere 5. Ovipositor with stylomere 1 fully sclerotized, stylomere 2 narrow, tapered apically ..... Subtribe Demetriina.
- 10' Tarsomere 4 with lobes short, less than half length of tarsomere 5. Stylomere 1 partially desclerotized, stylomere 2 broad, short, broadly rounded apically .... Subtribe Lebiina.

<sup>3</sup>Habu (1967: 250) expressed doubt about including *Celaenephes* Schmidt-Goebel in the Dromiina because of the setose stylomeres 1 and 2 of its females. Thus it would not key out above. Bates (1892: 156) included this genus among the cymindines, along with several other genera that were subsequently assigned to the Dromiina (Csiki, 1932). *Celaenephes* is clearly not a dromiine, and we believe that the stylomeres of its females are too plesiotypic for the genus to be included in the Cymindina. It may be a platynine, or it may represent a separate lineage of Lebiini that will require establishment of another subtribe.

19



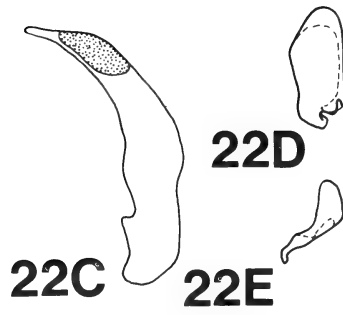
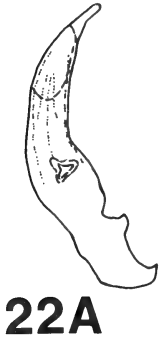
20



21

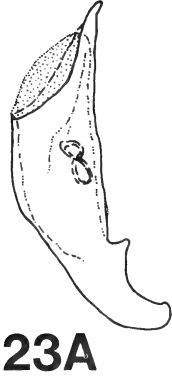


Figs. 19-21. Photographs of Pericalina, genus *Thyreopterus*.—Habitus, dorsal aspect. 19, *T. (Thyreopterinus)* species? (SBL = 5.38 mm); 20, *T. (sensu stricto) kivuanus* Basilewsky. (SBL = 6.30 mm); 21, (*Selenoritus*) *ptolemaei* (Alluaud) (SBL = 5.32 mm).

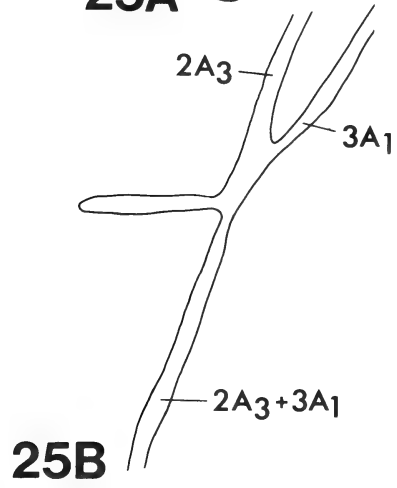
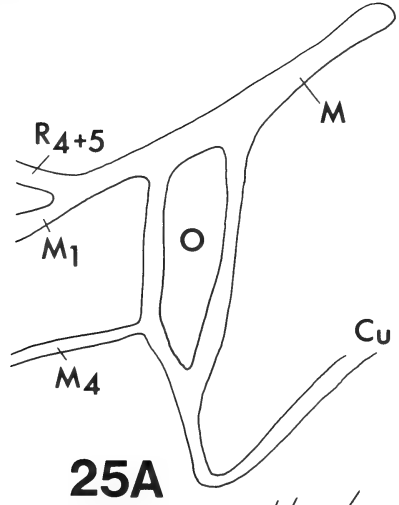


**22D**

**22E**



1mm



Figs. 22–24. Line drawings of structures of Pericalina, genus *Thyreopterus*.—Male genitalia. Fig. 22: *T. (Thyreopterinus)* species, A, B, C—median lobe, left lateral, ventral, and right lateral aspects, respectively, D and E, parameres, left and right, respectively, ventral aspect. Fig. 23: *T. (sensu stricto) kivuanus* Basilewsky —A and B, median lobe, left lateral, and ventral aspects, respectively; C and D, parameres, left and right, respectively, ventral aspect. Fig. 24: *T. (Selenoritus) ptolemaei* (Alluaud)—A and B, median lobe, left lateral and ventral aspects, respectively; C and D parameres, left and right, respectively, ventral aspect. Fig. 25. Line drawings of structures of Apenina.—Wing cells and surrounding veins of *Cymindoidea (sensu stricto) indica* Schmidt-Goebel, left wing: A, oblongum cell; B, wedge cell. Legend: cells—O, oblongum, W, wedge; veins—A, Anal; Cu, Cubital; M, Median; R, Radial.

## Tribe LEBIINI, Subtribe PERICALINA

Two genera (*Selenoritus* Alluaud, 1917, and *Leptosarcus* Péringuey, 1896), described originally as cymindines, are more appropriately assigned to the Pericalina because adults of each genus exhibit the diagnostic features of this subtribe: extended mouthparts (including elongate labrum), pair of suborbital setae, laterally displaced penultimate umbilical setigerous puncture of an elytron (Fig. 27B), stylomere 2 relatively small, falcate, with three large dorsal setae, and without a ventral preapical sensory furrow or nematoid setae (Figs. 28A-C).

Within the Pericalina, we place both of these genera in the thyreopteroid assemblage: *Selenoritus*, because it is actually a member of *Thyreopterus*; and *Leptosarcus* because stylomere 2 of the ovipositor lacks nematoid setae.

Jeannel (1949: 975) included *Selenoritus* in the tribe Thysanotini, subfamily Calleiditae, along with the Madagascan endemic genera *Antimerina* Alluaud, *Thysanotus* Chaudoir, and *Madecassina* Jeannel. External features of adults of these genera (seen in the MCZ) confirm that they are pericalines, and absence of nematoid setae from stylomere 2 of females of *Antimerina elegans* Alluaud, and *Thysanotus alluaudi* (Jeannel) provide the basis for assigning this geographical complex of genera to the thyreopteroid assemblage. Basilewsky (1953a: 10) suggested that Thysanotini should be included in the Thyreopteridae, but Ball (1975:147), on the basis of study of descriptions and illustrations, suggested that such a grouping would be incorrect. This group could be near the base of the stock that gave rise to the thyreopteroid radiation on Madagascar.

*Selenoritus* Alluaud, 1917

Figs. 21-22

*Selenoritus* Alluaud, 1917: 103. GENERITYPE: *Selenoritus ptolemaei* Alluaud, 1917: 104 (monotypy). LECTOTYPE male (here selected), labelled: MUSEUM PARIS MONTS ROUWENZORI zone des forêts Makitawa (2660 m) Ch. Alluaud 1909 [blue paper]; TYPE [red paper]; Museum Paris coll. Ch. Alluaud [blue paper]; *Selenoritus ptolemaei* Alluaud Type [white paper, with blue strip across top]. [MNHP]. PARALECTOTYPE male, similarly labelled in Musée d'Afrique Centrale, Tervuren.— Burgeon, 1937: 356.

*Selenorites* (misspelling) Jeannel, 1949: 975.— Basilewsky, 1962: 300 and 321.

*Notes about type material.*— The type locality of *S. ptolemaei* is more fully specified, as follows: ZAIRE, Mount Ruwenzori, east versant, in forest above the shelter, beneath peak of Makitawa, between 2600 and 2800 meters (Alluaud, 1917). Alluaud (1917: 103-104) provided a detailed description of external features of type specimens. His basis for claiming a relationship of this species to the cymindines is a combination of these features: truncate elytra, not covering apex of abdomen; broad paraglossae, clearly extended beyond apex of ligula; and denticulate tarsal claws.

Alluaud lists the following features as diagnostic of *Selenoritus*: disc of elytra more convex; elytra more ovoid with humeri more rounded, and basal groove not sinuate between humeri and scutellum; posterior pair of supraorbital setigerous punctures far removed posteriorly on occiput; antennomere 3 with more than apical setae; lateral margins of pronotum without setigerous punctures; and posterior tarsi with tarsomeres 1-5 filiform, not dilated nor grooved dorsally, elongate and subequal to one another. Most of these character states, however, appear in the pericaline genus *Thyreopterus* (*sensu lato*) as pointed out in conversation by Dr. P. Basilewsky, who had previously recognized the similarities between members of these two taxa.

Pectinate tarsal claws and small size place *Selenoritus* near the subgenus *Thyreopterinus* Alluaud.

Character states that distinguish adults of *Selenoritus* from those of *Thyreopterinus* are: small eyes (Fig. 21; cf. Fig. 19); posterior pair of supraorbital setigerous punctures clearly behind posterior margins of compound eyes; pronotum without posterior pair of setigerous punctures (members of both groups lack the anterior pair); basal ridge of elytron not extended to sutural margin, but terminated near base of interneur 4; metathorax and hind wings reduced. Small eyes, loss of setae, and reduced metathorax and hind wings seem to be adaptations associated with life in montane environments, and the position of the posterior pair of supraorbital setigerous punctures is probably the result of reduction of eyes, rather than posterior migration of the setigerous punctures. These differences might have evolved relatively recently, and thus do not constitute evidence that *S. ptolemaei* is phylogenetically old. Instead, this species may be only a moderately specialized member of *Thyreopterinus*.

On the other hand, many montane-adapted stocks seem to be relics of older stocks that have been replaced in the lowlands by later evolving relatives. Until the relationships of *Thyreopterinus* and *Selenoritus* can be more fully resolved, it seems as well to treat the two groups as separate subgenera of *Thyreopterus*. Evidence supporting this decision is provided by details of stylomere 2 of the ovipositor, for a combination of number and length of ensiform seta and form of these sclerites themselves distinguish females of these groups from one another. See Table 1 for details.

Male genitalia of *Selenoritus ptolemaei* are also markedly different from those of the one species of *Thyreopterus* examined (Fig. 24; cf. Fig. 23). In males of both *S. ptolemaei* and *T.*

TABLE 1.  
COMPARISON OF FEATURES OF STYLOMERE 2 OF THE OVIPOSITOR OF  
FEMALES OF SUBGENERA OF *THYREOPTERUS* DEJEAN

NAME OF SUBGENUS	STYLOMERE 2			
	No.	Ensiform Setae	Form	Apical Portion
		L. dorso-medial seta		Width
<i>Thyreopterus (sensu stricto)</i>	2	long	slightly falcate	markedly narrowed
<i>Thyreopterinus</i> Alluaud	3	long	markedly falcate	markedly narrowed
<i>Selenoritus</i> Alluaud	2	short	slightly falcate	wide

(*sensu stricto*) *kivuanus*, the apical orifice of the median lobe is slightly left of the mid-line; in males of *Thyreopterinus* species, it is to the right. However, such differences are common among pericalines, and their evaluation must be made in terms of additional species of subgenus *Thyreopterinus*.

*Thyreopterus (Selenoritus) ptolemaei* Alluaud, 1917, new combination

Figs. 21-22A, C

**Description.**— Habitus as in Fig 21. Standardized body length 6.20 mm. (lectotype; other specimens of similar size). Form pterostichoid or agonoid, slender.

Color generally rufo-piceous dorsally, more rufous ventrally, palpi, antennae and legs flavous. Elytra each with three groups of rufo-flavous marks: one group in basal 0.20 on intervals 2, 3, 6, 7, and 8; one group medially on intervals 7 and 8; and one group in apical 0.80 on intervals 2-8.

Microsculpture of dorsum. Head and elytra, with meshes isodiametric, those of elytra slightly shingled; pronotum with meshes transverse.

Luster. Surface generally shining.

Head. Clypeus longer than average; anterior margin concave; bipunctate, each puncture in longitudinal groove extended to posterior margin. Frons with impressions broad and shallow, each side with single longitudinal ridge; vertex slightly convex. Posterior pair of supraorbital setigerous punctures well posterad of posterior margin of compound eyes. Temples not extended.

Eyes. Reduced. Paragenae at narrowest less than width of antennal scape.

Antennae. Length average: scape slightly longer than antennomere 3, and slightly broader; outer antennomeres longer than wide (ant. 9 l/w— 3.00). Scape with single seta; pedicel with terminal ring of setae; antennomere 3 generally sparsely setose; remaining antennomeres setose.

Mouthparts. Labrum longer than average, tapered anteriorly. Mandibles elongate, slender (not studied in detail). Maxilla: stipes with several setae; palpus slender, palpomere 4 distinctly longer than 3; apical margin truncate, narrow. Labium: mentum with well developed tooth; ligula narrow, bisetose apically; paraglossae broad, extended clearly beyond apex of ligula; palpi slender, palpomere 2 bisetose; palpomere 3 with apical margin truncate.

Pronotum. Without lateral setae. Dorsal surface generally sparsely setose, setae short. Form slender, elongate, sides markedly sinuate posteriorly; anterior margin concave, angles short but distinctly set off; basal margin truncate. Sides moderately elevated, lateral grooves narrow, indistinctly isolated from posterior lateral impressions by convexity; median longitudinal impression shallow; anterior and posterior transverse impressions evident, but broad.

Prosternum. With few setae at apex of intercoxal projection.

Metepisternum. Short, almost quadrate.

Elytra. Slightly explanate, widest point evidently behind middle; humerus broadly rounded; basal ridge terminated near base of interneur 4, not extended to suture; apical margin sinuately truncate. Surface sparsely punctate, setae short. Parascutellar setigerous punctures present. Interneurs terminated before apex, shallow; intervals slightly convex. Umbilicate punctures 16, penultimate puncture slightly displaced laterally. (Lectotype with right elytron broken and detached).

Hind wings. Markedly reduced.

Legs. Average, generally. Tibial spines reduced, as usual for pericalines. Anterior femur with numerous setae ventrally. Anterior tibia with terminal spur thickened. Claws long, each with 4-5 pectinations. Anterior tarsomeres without adhesive vestiture.

Abdomen. Sterna average, sternum 6 with four setae near posterior margin.

Male genitalia. Median lobe (Figs. 22A-C) short, broad; apical portion in ventral aspect short, rounded; dorsal surface extensively sclerotized; apical orifice long, inclined to left. Internal sac with narrow sclerotized rim apically, otherwise unarmored. Left paramere with apical margin sinuate-truncate. Right paramere with apex acute. (Cf. Figs. 23A-C and 24A-C)

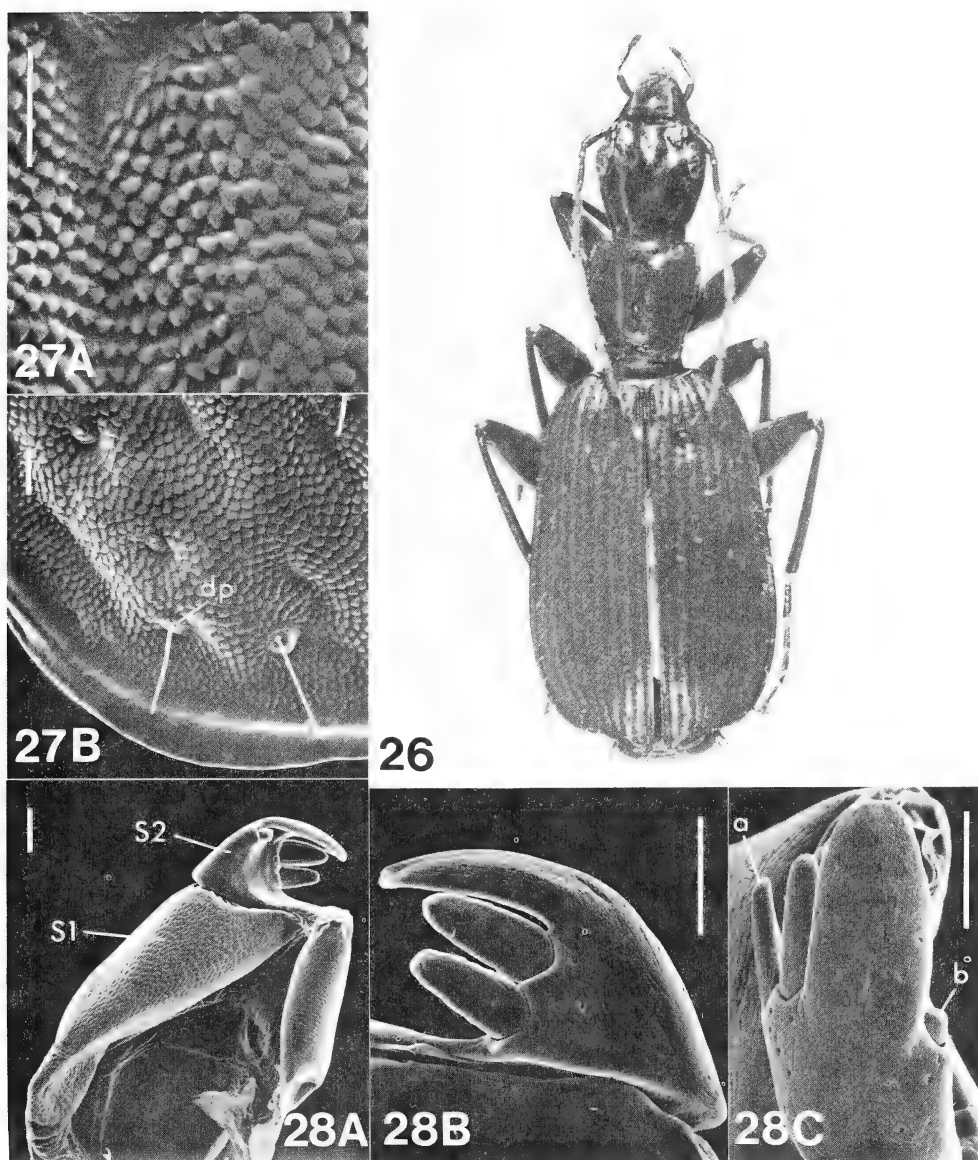
Ovipositor. Stylomeres 1 and 2 subequal in length. Stylomere 2 elongate, hardly curved, dorsally with two broad ensiform setae; without nematoid setae.

**Geographical distribution and habitat.**— This species is known from the higher slopes of Mt. Ruwenzori, Zaire. Two specimens were collected in dead bamboo.

**Material examined.**— We have seen the types and three additional specimens, as follows: Two males— Kilindera, north face of Ruwenzori, 2750 m., VII- VIII. 1974 R. P. M. Lejeune (MACT). Female— Vallee Mont Mulungu, Massif Ruwenzori, 2600 m., 29.11.1957, P. Vanschuytbroeck (MACT).

We also examined superficially material representing five additional species of *Thyreopterus (sensu stricto)* and four additional species of subgenus *Thyreopterinus*, from





Figs. 26–28. Photographs of *Pericalina*, genus *Leptosarcus*.—Fig. 26: *L. hessei* Basilewsky, habitus, dorsal aspect (SBL = 12.86mm). Figs. 27–28. SEM photographs of elytra and stylomeres of *L. porrectus* Péringuey. Fig. 27: Left elytron, microsculpture, dorsal aspect—A, discal area; B, preapical area. Fig. 28 ovipositor, left stylomeres; A, stylomeres 1 and 2, medial aspect; B, stylomere 2, lateral aspect; C, stylomere 2, apico-ventral aspect. Scale bars, Figs. 27–28 = 50  $\mu$ m. Legend, elytra: dp, penultimate umbilical puncture, displaced toward lateral margin. Legend, stylomeres: a, lateral ensiform seta; b—medial ensiform seta; S1, stylomere 1; S2, stylomere 2.

collections of CAS. Fig. 20 illustrates the habitus of *T. (sensu stricto) kivuanus* Basilewsky.

*Leptosarcus* Péringuey, 1896

*Leptosarcus* Péringuey, 1896: 218. GENERITYPE: *Leptosarcus porrectus* Péringuey, 1896: 219 (monotypy).—Basilewsky, 1954a: 83.

Basilewsky (1954a) studied the few specimens of *Leptosarcus* that were available, including type material of *L. porrectus* Péringuey (type locality—Vonstantia, Cape Province, South Africa). He provided a description of adult features generally satisfactory for recognition of specimens, and figured heads, labra, labia, and male genitalia. He also described a second species, *L. hessei* (type locality—Zululand). To Basilewsky's characterizations, we add the following observations.

Microsculpture of the elytra is shingled (Figs. 27A, B), like that of some of the more highly derived members of the New World genus *Phloeoxena* (see Ball, 1975), and is quite unlike the smoother microsculpture characteristic of the elytra of cymindine adults. The penultimate umbilical setigerous punctures of the elytra are displaced laterally (Fig. 27B). Stylomeres 1 and 2 (Figs. 28A-C) are typical of the thyreopteroid Pericalina. Probably adults of *Leptosarcus* should be sought in the types of habitats occupied by *Phloeoxena* adults; *i.e.*, in association with fallen logs, or standing trees with loose or scaly bark, in wet forests.

We conclude that general similarity in form and size between adults of *Leptosarcus* and of *Hystrichopus (sensu stricto)* is convergent. Males of *Leptosarcus* have anopic median lobes as have males of *Cymindis*, but this feature is plesiotypic, and is thus not of use in establishing relationships.

This genus seems to be relict for several reasons: low diversity; seemingly without close relatives among pericalines; adults brachypterous, and metathorax reduced; and geographical distribution peripheral to the main area (tropics) of the Pericalina.

*Material examined.*—We have seen seven specimens representing both known species, all from the collections of the South African Museum, and all collected at localities in the Union of South Africa, as follows.

*Leptosarcus porrectus* Péringuey

Figs. 27-28

Male, holotype, labelled: C.T. 8.26 type; HOLOTYPUS [red paper]; *Leptosarcus porrectus* P; *Leptosarcus porrectus* Per Basilewsky vid 1953. Male, paratype, from same locality as holotype, and also seen by Basilewsky. Female, same locality, det. by Basilewsky, 1953. Female, Hott- Holl Mts. 4000 f., Caledon C.C., Bernard 1916; det. by Basilewsky, 1953.

*Leptosarcus hessei* Basilewsky

Fig. 26

Female HOLOTYPUS [red paper]; Mt. Kendhla forest Zululand; *Leptosarcus hessei* n.sp. P. Basilewsky det. 1953.

Tribe LEBIINI, Subtribe APENINA

This subtribe was erected by Ball (1982). Diagnostic character states are: head without suborbital setigerous punctures; elytron with penultimate umbilical puncture laterad of antepenultimate and ultimate umbilical punctures; tibiae and tarsi relatively slender;

ovipositor, (Figs. 38, 39A, B) with stylomere 1 much longer than 2, asetose; stylomere 2 markedly curved, apex of blade pointed; two large ensiform setae on dorsal margins; preapical sensory furrow and associated setae absent.

**Description.**— The following statements indicate range of variation of selected features useful for recognizing apenine adults, and for determining relationships of taxa.

**Color.** Various, but mostly somber: dorsum dark rufous to black, elytra with or without paler spots; venter piceous to testaceous; legs and palpi of most specimens pale— rufous to testaceous, though femora of some specimens as dark as ventral surface.

**Microsculpture.** Labrum and clypeus with meshes isodiametric. Dorsum of head with meshes isodiametric, or microlines effaced; venter with meshes transverse. Pronotum with meshes isodiametric, or transverse, or microlines effaced. Lateral and ventral thoracic sclerites with meshes transverse (characteristic of most groups) or isodiametric. Scutellum with meshes isodiametric (characteristic of most groups) or transverse. Elytra with meshes isodiametric, transverse, or effaced. Abdominal sterna with meshes transverse, or transverse medially, and isodiametric laterally.

**Luster.** Surface of head and thorax shining to dull; surface of elytra and abdominal sterna iridescent, shining, or dull.

**Macrosculpture.** Surface generally smooth, except as noted. Head (frons and vertex), pronotum, and elytral intervals smooth, or variously transversely ridged and grooved. Surface impunctate, or covered with coarse punctures.

**Vestiture.** Surfaces of adults of most taxa glabrous, but *Trymosternus* adults generally setose. Antennomeres 1 and 2 with setae confined to apex, or generally setose; antennomere 3 with setae confined to apical 0.50, or generally setose; antennomeres 4–11 generally setose. Tarsomeres dorsally setose.

**Fixed setae.** Average for lebiine adults: labrum with six long marginal setae, clypeus with one pair; head and pronotum each with two pairs; elytra each with two discal setae in interval 3, parascutellar and preapical setae, and 15 umbilical setae along lateral margin; penultimate umbilical seta displaced laterally of an imaginary line extended between antepenultimate and ultimate umbilical punctures. Legs (anterior, middle, and posterior) with number of setae as follows: coxae— 0–1, 2–5, 2; trochanters— 1, 1, 1; femora— 2 (posterior face), 3–5 (anterior face), 2 (anterior face). Sternum VII with two setae in males, and two or four setae in females.

**Head.** Clypeus transverse, anterior margin of each truncate or slightly concave. Frontal impressions shallow, indistinct. Sub-antennal ridge average or prominent. Eyes: orbicular, convex, visible in ventral aspect; or reduced, longer than wide, flattened, ventral margin obliquely truncate, and not visible in ventral aspect. Insertion of antennal scape close to or remote from anterior margin of adjacent eye.

**Antennae.** Average for lebiine adults: filiform, flagellar antennomeres sub-cylindrical, distinctly longer than wide, antennomere 2 short, antennomere 3 longer than 4.

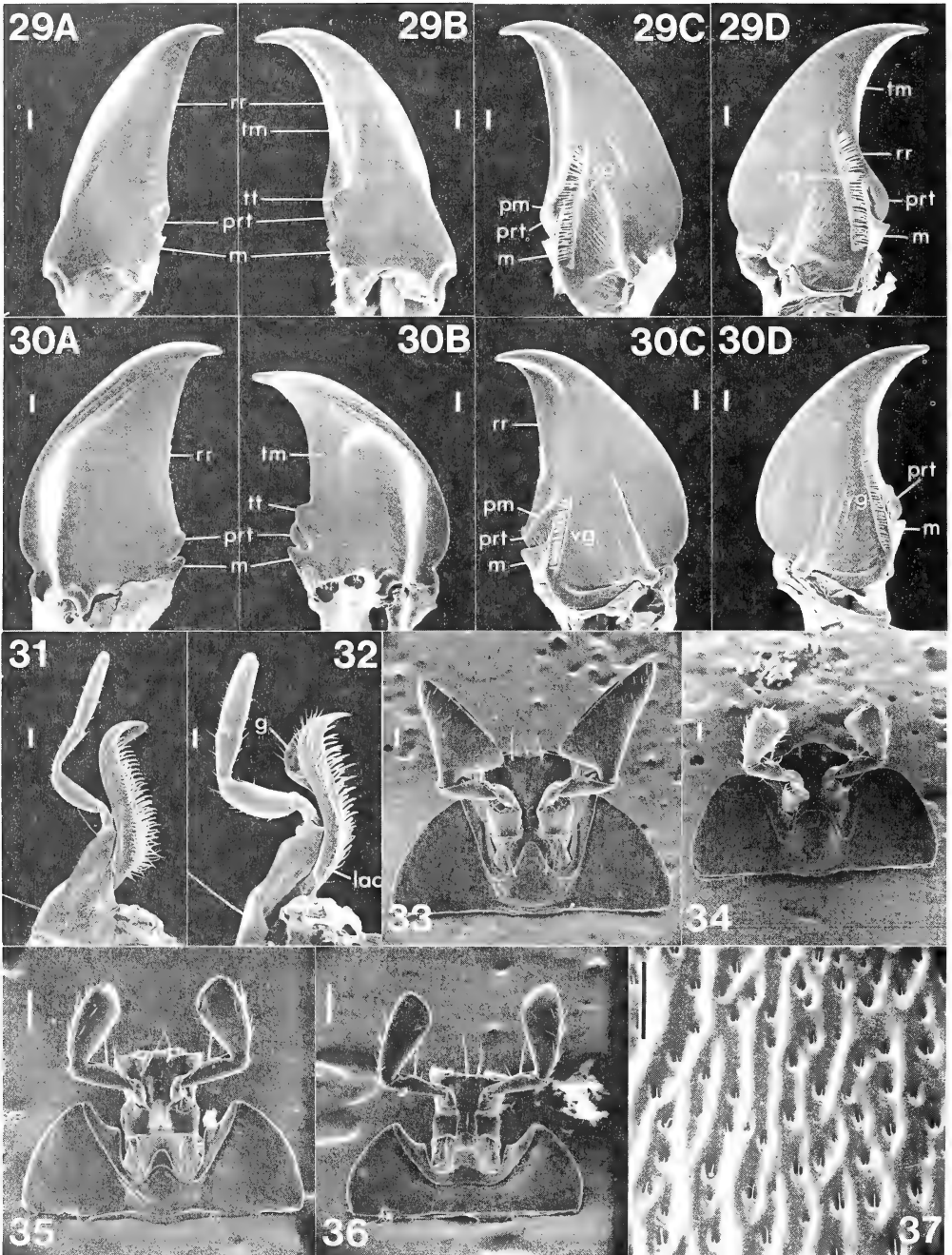
**Mouthparts.** Labrum transverse, anterior margin truncate or slightly concave. Mandibles. Left and right mandible about same shape, overall. Left mandible (Figs. 29A, C, 30A, C) with terebral margin reduced, no terebral tooth. Cutting edge retinacular ridge; posterior retinacular tooth small, not divided; ventral retinacular ridge blunt; premolar triangular; premolar ridge well developed, sharp. Right mandible (Figs. 29B, D - 30B, D) with terebral margin cutting edge, terebral tooth blunt, large; retinacular ridge well developed, anterior and posterior teeth blunt; ventral ridge not developed; premolar tooth triangular, sharp at apex; ventral groove extended basad, to premolar area. Maxillae, average for lebiine adults: lacinia with (Fig. 32), or without (Fig. 31) apico-lateral setae; palpomeres slender, 4 with apical margin truncate, slightly longer than 3, markedly longer than 2. Labium: mentum (Figs. 33–36) bisetose, with lateral lobes pointed apically (Fig. 33) or broadly rounded (Fig. 34), tooth well developed, pointed apically (Figs. 33–35), or absent (Fig. 36); glossal sclerite with apical margin broad, sub-truncate, bisetose (or quadrisetose, median two setae close together, much shorter than lateral pair); paraglossae fused to glossal sclerite, apical margins finely setose, hardly extended beyond apex of glossal sclerite; palpomeres 1 and 2 slender, palpomere 3 more (Fig. 33) or less (Fig. 36) broadly securiform, more so in males than in females.

**Thorax.** Pronotum with sides rounded, more constricted basally than apically (or markedly cordate, constricted basally, sides strikingly sinuate basally); base lobate medially (or almost truncate); anterior angles broadly rounded, posterior angles sharp, prominent; disc slightly convex, median longitudinal impression sharply defined, anterior and posterior transverse impressions hardly evident; posterior lateral impressions shallow, indistinct. Prosternum with intercoxal process immarginate. Metepisternum distinctly longer than wide, lateral margin 1.5 times longer than anterior margin (or almost as long as wide, anterior and lateral margins subequal).

**Elytra.** Average in form; humeri prominent, extended slightly forward, basal ridge marginal, extended to edge of scutellum. Apical margin obliquely subtruncate. Interneurs average for carabids (or broader than average), punctate; scutellar interneur well developed. Intervals slightly convex (or alternate odd-numbered intervals sub-carinate to carinate, raised above even-numbered intervals).

**Wings.** Well developed (or short stubs); wedge cell absent (Fig. 25B), oblongum cell average (Fig. 25A) (or reduced, or absent). Venation otherwise normal for lebiines.

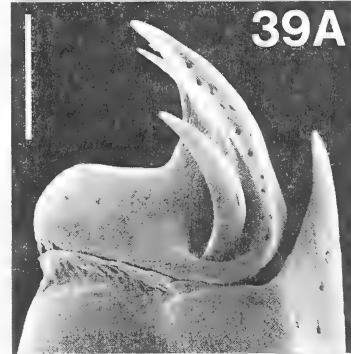
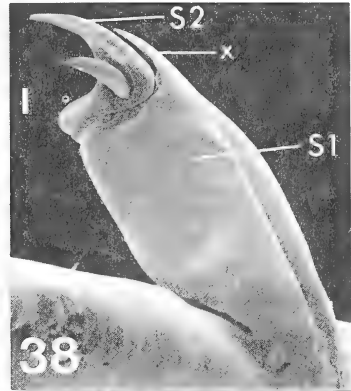
**Legs.** Average for carabids. Middle tibia with spines of outer row numerous, extended length of margin (or spines few, located in apical 0.25). Tarsal claws pectinate. Tarsomere 4 notched, but not bilobed. Male with front tarsomeres 1–3 ventrally with biseriate adhesive vestiture.



Figs. 29–37. SEM photographs of structures of *Apenina*.—Figs. 29–30, mandibles—A and C, left, dorsal and ventral aspects, respectively, B and D—right, dorsal and ventral aspects, respectively, of: 29, *Cymindoidea (sensu stricto) indica* Schmidt–Goebel; 30, *Apenes (sensu stricto) lucidula* Dejean. Figs. 31 and 32, right maxilla, ventral aspect of: 31, *C. indica*; 32, *A. lucidula*. Figs. 33–36, labium, ventral aspect of: 33, *C. indica*; 34, *A. lucidula*; 35, *A. (Sphalera)* species; and 36, *A. (Sphalera) postica* (Dejean). Fig. 37, *C. indica*: head, microsculpture, dorsal aspect. Scale bars = 100  $\mu$ m. Legend, mandibles: m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; tt, terebral tooth; vg, ventral groove.



40



Figs. 38–40. Photographs of Apenina.—Figs. 38–39: SEM photographs of ovipositor, left stylomeres. Fig. 38: *Cymindioidea (sensu stricto) indica* Schmidt-Goebel, stylomeres 1 and 2, lateral aspect, Fig. 39: *Apenes (sensu stricto) lucidula* Dejean: A and B, lateral and apico-ventral aspects, respectively. Scale bars = 50  $\mu\text{m}$ . Fig. 40: *Cymindioidea (Habutarus) papua* (Darlington), habitus, dorsal aspect (SBL = 4.81 mm.). Legend, stylomeres: a, lateral ensiform seta; S1, stylomere 1; S2, stylomere 2; x, projection of stylomere 1.

Abdomen. Sterna II–VII average. Female: tergum VIII broadly membranous medially; sternum VIII broadly membranous medially, lateral apodemes short; tergum X completely sclerotized.

Male genitalia. Median lobe cylindrical, elongate, slightly curved ventrally. Apical portion slender, without projections, quite short, but varied in length; anopic, orifice either dorsal, or dorso-lateral, toward left side. Internal sac with vestiture of smaller (or larger) microtrichia; with or without long, coiled, flagellum. Left paramere average for lebiomorph males; right paramere, though reduced, large for lebiomorphs.

Ovipositor (Figs. 38 - 39A, B). Valvifer markedly transverse, narrow. Stylomere 1 about twice length of stylomere 2, ventral apical angle markedly produced beyond base of stylomere 2, asetose; stylomere 2 with base extended dorsally as lobe; apical portion sword-like, apex pointed; two very large ensiform setae dorsally; ventral surface with two rows of sensory pits; without ventral preapical sensory furrow and associated setae.

**Classification.**— Included in the Apenina are three genera: *Apenes* LeConte (subgenus *Apenes* and *Sphalera* Chaudoir); *Cymindoidea* Castelnau (subgenus *Cymindoidea*, *Platytarus* Fairmaire, and *Habutarus*, new subgenus); and *Trymosternus* Chaudoir. Reduction of the oblongum cell of the hind wing is an autapotypic feature establishing monophyly of the New World genus *Apenes*. Monophyly for the Old World assemblage of *Trymosternus* and *Cymindoidea sensu lato* is established by an autapotypic feature of the internal sac of male genitalia: possession of a moderately to very long and coiled flagellum. In the Old World assemblage, monophyly of *Trymosternus* is established by a combination of: integument generally setose, and labial palpomere 2 plurisetose.

We have not been able to establish monophyly of *Cymindoidea*, for we have not identified synapotypic features for all three subgenera. *Cymindoidea* and *Platytarus* are linked by a quadripunctate glossal sclerite, broadened pronotum, and rugose dorsum. We could make *Cymindoidea* monophyletic by including in it *Trymosternus*, but we suspect this decision would not be acceptable to our European colleagues, who seem generally to prefer retention of traditionally recognized taxa, in spite of phylogenetic considerations. We could also achieve the desired result by excluding *Habutarus*, but this would require establishment of a monobasic genus, and we are reluctant to do this. The compromise (which yields a cladistically unacceptable genus) is to include *Habutarus* in *Cymindoidea* on the basis of a symplesiotypic feature: the glabrous integument.

**Geographical distribution.**— This subtribe has a Gondwanian distribution pattern, with a sister group on each side of the Atlantic Ocean, mainly in the Southern Hemisphere and tropics.

### Key to Genera and Subgenera of Subtribe Apenina

- 1 (0) Dorsum setose. Eyes reduced, not visible in ventral aspect. Antennal fossa remote from anterior margin of eye. Elytron with humerus sloped. Metepisternum quadrate, wings represented by short stubs. Metasternum with deep pit near middle coxae ..... *Trymosternus* Chaudoir, p. 128
- 1' Dorsum glabrous, except for normal fixed setae. Eyes various. Antennal fossa close to or remote from anterior margin of eye. Elytron with humerus broadly rounded. Metepisternum and wings various. Metasternum without pit near middle coxae ..... 2.
- 2 (1') Glossal sclerite with four setae. Dorsal surface modified, either coarsely and irregularly sculptured and punctate, or microsculpture with lines deep, sculpticells convex, luster dull, and discal elytral intervals keeled ..... 3.
- 2' Glossal sclerite with two setae. Dorsal surface unmodified, smooth, elytral intervals more or less flat ..... 4.
- 3 (2) Microsculpture of thoracic pleura and sterna with meshes isodiametric.

- Antennomeres 1 and 2 generally setose. Elytron with odd-numbered intervals carinate. Fossa of antenna and anterior margin of adjacent eye separated by wide gap ..... *C. (Platyтарus)* Fairmaire.
- 3' Microsculpture meshes of thoracic pleura and sterna transverse. Antennomeres 1 and 2 with setae near apices, only. All elytral intervals non-carinate. Antennal fossa and anterior margin of adjacent eye close together ..... *C. (Cymindoidea)* Castelnau p. 126
- 4 (2') Metepisternum quadrate, wing represented by short stub. Dorsum of head with irregular shallow grooves and irregular ridges. Range— New Guinea ..... *C. (Habutarus)* new subgenus, p. 127
- 4' Metepisternum elongate, wing long, normally developed. Head with dorsum smooth or ridged. Range— Neotropical and southern Nearctic Regions ..... 5.
- 5 (4') Head with dorsum ridged or coarsely punctate ..... *A. (Apenes)* LeConte, p. 125
- 5' Head with dorsum smooth, not punctate or ridged ..... *A. (Sphalera)* Chaudoir.

*Apenes* LeConte

Figs. 30, 32, 34-36, and 39

*Apenes* LeConte, 1851: 174. GENERITYPE: *Cymindis lucidula* Dejean, 1831:320 (subsequent designation, by Motschulsky, 1864: 240, table).— LeConte, 1861: 24.— Chaudoir, 1875: 21, 35.— Horn, 1881: 156.— 1882: 156.— Bates, 1883: 188.— Blatchley, 1910: 147, 154.— Ball, 1960: 161.— Lindroth, 1969a: 1087.— Reichardt, 1977: 443

*Sphenopalpus* Blanchard, 1853: 32. GENERITYPE: *Sphenopalpus parallelus* Blanchard, 1853: 32 (= *Cymindis aenea* Dejean, 1831: 319) (monotypy).— Chaudoir, 1871: 385.

*Sphenopselaphus* Gemminger and Harold, 1868: 299. Unjustified emendation of *Sphenopalpus*.

*Nominus* Motschulsky, 1864: 240 (table). GENERITYPE: *Cymindis punctulata* Dejean, 1831: 316 (= *Cymindis sinuata* Say, 1823: 8) (original designation by Motschulsky, 1864: 240, table).— Chaudoir, 1875: 42.

*Malisus* Motschulsky, 1864: 240 (table). GENERITYPE: *Cymindis variegata* Dejean, 1825: 217 (original designation).

*Didymochaeta* Chaudoir, 1875: 50. GENERITYPE: *Didymochaeta hamigera* Chaudoir, 1875: 53 (here designated).

*Sphalera* Chaudoir, 1875: 54. GENERITYPE: *Cymindis postica* Dejean, 1831:317 (monotypy). NEW SYNONYMY.

*Notes about synonymy.*— Chaudoir (1875) recognized four genus-group taxa that we include in *Apenes*: *Apenes (sensu stricto)*; *A. (Malisus* Motschulsky); *Didymochaeta* Chaudoir, 1875; and *Sphalera* Chaudoir, 1875. Bates (1883: 189) synonymized the first three names because the taxa were based on “slight characters (*Malisus*) on general form and facies, (*Didymochaeta*) on the narrow ligula and tooth of mentum”. To these names, we add *Sphalera* Chaudoir, this taxon being based on absence of a mental tooth (Fig. 36). This feature involves a minor desclerotization. Otherwise, adults are strikingly like those included in *Didymochaeta*.

For the atypical subgenus, we choose the name *Sphalera* (rather than *Didymochaeta*) because the former has fewer letters, and is thus easier to write, if not to remember.

*Recognition.*— Adults of this genus are distinguished from other apenines by the following combination of character states: glossal sclerite with a single pair of setae, dorsum glabrous, metepisternum longer than wide, hind wings normally developed, metasternum smooth, without a pit near the middle coxae. Additionally, males are distinguished by lack of a flagellum of the internal sac.

*Description.*— Character states mostly as for subtribe, with restrictions or exceptions as follows.

Microsculpture. Dorsum of head with meshes isodiametric. Pronotum and elytra with meshes isodiametric or transverse.



Vestiture. Surface generally glabrous. Antennomeres 1 and 2 with setae confined to apex, antennomere 3 with setae confined to apical 0.50.

Head. Sub-antennal ridge average. Eyes orbicular, prominent, ventral margin rounded. Antennal fossa close to antero-ventral margin of eye. Flagellar antennomeres distally longer than wide or length and width subequal, and antenna short.

Mouthparts. Labium: mentum with lateral lobes broadly rounded or pointed apically; tooth absent or present and bluntly or sharply pointed; glossal sclerite bisetose; palpomere 2 bisetose; palpomere 3 slightly to markedly securiform.

Thorax. Pronotum with sides rounded, or sinuate posteriorly; base lobate medially. Metepisternum distinctly longer than wide.

Elytra. Interneurons average. Intervals slightly convex.

Wings. Well developed: oblongum cell shortened (stalked) or absent.

Male genitalia. Internal sac without coiled flagellum.

**Classification.**— The species of *Apenes* are here grouped into two subgenera: *Apenes* (*sensu stricto*), including the species of *Malisus*), adults larger, body thicker, more terete, with head grooved or coarsely punctate, and oblongum cell of wing stalked; and *Sphalera* (including *Didymochaeta*), adults smaller, flatter, with head smooth (frontal impressions extended diagonally to anterior supraorbital setigerous punctures), and wings without oblongum cell.

**Phylogenetic considerations.**— External features of adults of subgenus *Sphalera* seem more plesiotypic, but absence of the oblongum cell from the wing, and absence of a mental tooth are apotypic features. Conversely, adults of *Apenes* (*sensu stricto*) seem more derived in body form, but retain the oblongum cell. The more sculptured integument characteristic of *Apenes* (*sensu stricto*) adults is shared with adults of the Old World *Cymindoidea* (*sensu stricto*) and subgenus *Platyтарus*. This similarity is probably convergent.

**Geographical distribution.**— The range of *Apenes* extends from northern Argentina in South America, to southern Ontario in eastern North America.

### *Cymindoidea* Castelnau

Figs. 29, 31, 33, 37, 38, and 40

*Cymindoidea* Castelnau, 1832: 390. GENERITYPE: *Cymindis bisignata* Dejean, 1831: 322 (monotypy).— Andrewes, 1930: 140-141.— Basilewsky, 1961a: 154.— Csiki, 1932: 1490.— Jedlička, 1963: 462.

*Philotecnus* Mannerheim, 1837: 42. GENERITYPE: *Philotecnus stigma* Mannerheim, 1837: 42 (= *Cymindis bisignata* Dejean) (monotypy).

*Platyтарus* Fairmaire, 1850, XVII (Bull.), XVII. GENERITYPE: *Cymindis famini* Dejean 1826: 447. (original designation).— Basilewsky, 1961a: 165.— Antoine, 1962: 554.— Jedlička, 1963: 463.

**Notes about synonymy.**— Basilewsky (1961a: 154 and 165-166) provided relatively recent listings of references to the above genus-group names. Reasons for including *Cymindoidea* (*sensu stricto*) and *Platyтарus* in the same genus are given under "Classification".

**Recognition.**— Adults of this genus are distinguished from those of *Trymosternus* by the glabrous dorsum and unmodified metasternum. Additionally, adults of subgenus *Platyтарus* (the only group partially sympatric with *Trymosternus*) have four glossal setae, and flatter eyes. Adults of the Papuan subgenus *Habutarus* are like those of the New World subgenus *Apenes*, but the two groups are distinguished not only on the basis of wing development (see key) and geographical distribution, but males of *Habutarus* have a long flagellum in the internal sac that is characteristic of *Cymindoidea*.

**Description.**— Character states mostly as described for subtribe, with restrictions and exceptions as follows.

Head. Frons and vertex with longitudinal ridges and grooves, irregularly rugose (Fig. 37); with or without prominent supraocular ridges. Subantennal ridge prominent. Eyes orbicular or flattened, and longitudinally oriented; ventral margin straight or curved. Temples well developed. Antennal fossa close to or remote from anteroventral margin of eye. Flagellar antennomeres longer than wide.

Mouthparts. Maxilla: lacinia (Fig. 31) without setae on lateral preapical margin, few setae on ventral surface; mentum (Fig. 33) with lateral lobes pointed apically, tooth well developed, pointed apically. Glossal sclerite (Fig. 33) with two or four setae, for latter condition, median pair very close together basally; palpomere 3 markedly securiform, maximally so in



males.

Thorax. Metathorax normal, or reduced, with metepisternum quadrate.

Wings. Well developed, with oblongum cell not reduced (Figs. 25A, B), or brachypterous.

Legs. Spines of tibiae reduced.

Male genitalia. Internal sac with long coiled flagellum.

**Classification.**— Although Jeannel (1949: 947) included *Platyтарus* in the subfamily Calleiditae on the basis of reduced tibial spines of adults, other character states show that the group is correctly placed near *Cymindoidea* – where it was placed by previous authors. In fact, the only character states separating the two groups seem neither sufficiently numerous nor sufficiently important (they involve form and surface sculpture only) to accord generic rank to these groups. On the other hand, with antennae shifted forward, eyes flatter and seemingly more protected by the rest of the head, the body generally narrower and deeper, we believe that the species of *Platyтарus* occupy an ecological zone rather different from that occupied by the species of *Cymindoidea* (*sensu stricto*). On this basis, we accord subgeneric rank to these groups.

Adults of the new taxon *Habutarus*, described below, are superficially strikingly different from those of *Cymindoidea* and *Platyтарus*. Nonetheless, they have the basic attributes of *Cymindoidea*, and we prefer to emphasize similarities rather than differences. We do this by including *Habutarus* in *Cymindoidea* (*sensu lato*).

**Identification of species.**— Andrewes (1935: 202-204) provides keys to adults of the species of *Cymindoidea* (*sensu stricto*) and the subgenus *Platyтарus*. Basilewsky (1961a) provides keys to adults of the African species of *Cymindoidea* (pp. 155-158) and *Platyтарus* (pp. 166-168).

**Material examined.**— We have seen adults of the following: *Cymindoidea* (*sensu stricto*)— 19 specimens (two dissected; CAS), representing four Afrotropical and four Oriental species; *Platyтарus* – 41 specimens (two dissected, CAS), representing four species; and *Habutarus* – 17 specimens (three dissected, MCZ), representing *C. papua* (Darlington), all paratypes, from Dobodura, Papua, New Guinea.

**Geographical distribution.**— The range of this genus is discontinuous: *Cymindoidea* (*sensu stricto*) and *Platyтарus* are widespread in Africa and the Oriental Region, with the range of *Platyтарus* extended eastward to Indo-China and northward to Hong Kong, and that of *Cymindoidea* only as far as Burma (Jedlička, 1963: 462-463); *Habutarus* is known only from New Guinea, that is, the northern part of the Australian Region. Species of *Cymindoidea* (*sensu lato*) have not previously been recorded from the Indo-Australian Archipelago.

### *Habutarus*, new subgenus

Fig. 40

**GENERITYPE:** *Nototarus papua* Darlington, 1968: 186 (monotypy; here designated).

**Derivation of name.**— From the surname of Dr. Akinobu Habu; and “*tarus*”, one of the junior synonyms of *Cymindis*, and a name used in various combinations for cymindine-like forms. Features of the ovipositor provide the principal clue to determining the correct location of this taxon. Dr. Habu emphasized the importance of features of this structure in classification of Lebiini, and so we are pleased to dedicate this subgenus to him, in recognition of his contribution.

**Recognition.**— Adults of the single species included here resemble those of the Australian calleidine subgenus *Nototarus* Chaudoir (see below), but as indicated above, they have the basic attributes of the Apenina in general, and of *Cymindoidea* in particular.

**Description.**— Darlington (1968: 185-186) provides a good description of the type species of *Habutarus*. We draw attention here to certain features that are useful in comparing this group with other members of *Cymindoidea sensu lato*.

Habitus as in Fig. 40. Body size small (SBL ca. 5.5-6.0 mm.). Dorsal surface shining, lines of microsculpture fine, meshes of elytra irregular, from isodiametric to slightly transverse. Eyes and temples like those of *Cymindoidea* (*sensu stricto*), antennal fossae near anterior margins of eyes. Pronotum with base markedly narrower than maximum width, hind angles acute; median longitudinal impression rather wide and deep. Metathorax reduced, metepisternum subquadrate; brachypterous. Male genitalia and ovipositor average for *Cymindoidea sensu lato*.

*Habitat*.—Darlington (1968: 186) stated that adults of *C. papua* were collected from flood debris on rain forest floor.

*Phylogenetic relationships*.—Because of its plesiotypic character states (relatively unmodified dorsal integument, glossal sclerite with single pair of setae, and pronotum cordate), we believe that *Habutarus* must be closely related to the ancestral stock of *Cymindoidea sensu lato*, and thus remote from the other extant species of this genus. Geographical remoteness from the main range of the genus and reduced hind wings are also features suggesting a relict status for this subgenus.

### *Trymosternus* Chaudoir

*Trymosternus* Chaudoir, 1873: 106. GENERITYPE: *Cymindis onychina* Dejean, 1825: 217 (subsequent designation, by Antoine, 1962: 559). Seidlitz, 1887: 8.—1888: 8.—Bedel, 1906: 242.—Iakobson, 1907: 396.—Csiki, 1932: 1486.—Jannel, 1942a: 1057.—1949: 396.—Mateu, 1952: 109-141. 1958: 1-6.—Antoine, 1962: 559.

*Recognition*.—Adults of this genus are distinguished from other apenines by combination of a markedly cordate pronotum, metasternum with a deep pit near middle coxae, short (reduced) metepisternum, and generally setose integument.

*Description*.—Character states mostly as for subtribe, with restrictions and exceptions as follows. See Mateu (1952: 111-113) or Antoine (1962: 559) for a more detailed description.

Color. Body piceous to rufo-piceous; elytra concolorous.

Vestiture. Surface generally coarsely punctate, setose, including mandibular scrobes and antennomeres 1-3.

Head. Frons laterally with pronounced ridge each side. Sub-antennal ridge prominent. Eyes oblong, flattened. Temples prominent. Antennal fossa well in front of antero-ventral margin of eye. Flagellar antennomeres longer than wide.

Mouthparts. Labium: mentum with lateral lobes pointed apically; tooth acute at apex; glossal sclerite bisetose; palpomere 3 distinctly securiform.

Thorax. Pronotum cordate, sides markedly sinuate posteriorly; base subtruncate, not lobed medially. Metepisternum short. Metasternum with deep pit anteriorly, near middle coxae.

Elytra. Humeri distinctly narrowed. Interneurs average, though coarsely punctate. Intervals slightly convex.

Wings. Reduced to short stubs.

Legs. Middle and posterior tibiae with reduced spines, latter absent from lateral margins.

Male genitalia. Internal sac with coiled flagellum.

*Notes about identification of species*.—See Mateu (1952).

*Material examined*.—Three specimens (CAS): *Trymosternus onychinus* (Dejean), male; and *T. cordatus* Rambur, male and female.

*Geographical distribution*.—The range of the 10 species of this genus is confined to the mountains of the Iberian Peninsula and to North Africa north of Morocco and Oran (Mateu, 1952, 1958; Antoine, 1962). Only one polytypic species (*T. truncatus* Rambur) occurs in North Africa, and in that part of Spain immediately adjacent to Gibraltar. The other nine species are on the mainland, most of them in southern Spain, and most with markedly restricted geographical ranges. *Trymosternus onychinus* is wide-ranging (see Mateu, 1952: Fig. 4).

*Phylogenetic considerations*.—Antoine (1962: 560) regards this genus as highly evolved and isolated. Certainly, body form resulting in part from wing loss and in part from the striking lateral lobes of the pronotum exhibited by adults of some species, give this impression. However, the bisetose glossal sclerite, relatively unmodified elytral intervals, and restricted geographical range suggest that this genus is the survivor of an old stock. It was probably isolated for an extended period on the Miocene betico-rifian massif (Antoine, 1962: 560), where it differentiated. In post-Miocene time, it dispersed northward, attaining its present

range (Mateu, 1952: 117).

*Evolution of the Apenina: preliminary considerations.*— We are not in position to address this topic in detail, but some aspects of a general pattern seem clear enough to formulate a preliminary hypothesis in the form of a scenario.

The ancestral stock of the extant taxa, whose adults were like those of *Sphalera* and *Habutarus*, was widespread in Gondwana. Following the split which led to formation of South America and Africa, and thus to division of the ancestral stock of Apenina, the New World group differentiated as *Apenes*. In the Tertiary, various stocks dispersed northward, differentiating to produce the complex of extant species that presently inhabit Middle and North America and the West Indies.

In the Old World, events seem to have been more complex, for the distribution of extant taxa seems to suggest at least two major episodes of evolution: an early one, represented by taxa with limited ranges— *Trymosternus* (centered in the Iberian Peninsula), and *Habutarus* (known only from New Guinea); and a later episode, represented by centrant groups *Cymindoidea* and *Platyтарus*. We believe that the present centrant groups overran the ranges of the early-evolved taxa, displacing the latter from the central areas, and leaving only peripheral remnants. This does not explain absence of species of *Cymindoidea* (*sensu lato*) from the Indo-Australian Archipelago, but we expect that the group is represented there, though specimens have not yet been collected.

If our hypothesis is correct, the main islands of the Indo-Australian Archipelago will be populated by stocks of *Cymindoidea* (*sensu stricto*) or *Platyтарus*, and the peripheral islands (near New Guinea) by *Habutarus*. We also anticipate that the pattern we presently perceive will not be altered by subsequent discoveries. However, if it is altered by discovery of additional remnants of early-evolved groups in Africa or on the mainland of southeastern Asia, they will be residents of high altitude forests, and their adults will be brachypterous.

#### Subtribe CYMINDINA

We have seen specimens representing seven taxa of this group that are currently ranked as genera: *Cymindis* Latreille, 1806; *Hystrichopus* Boheman, 1848; *Plagiopyga* Boheman, 1848; *Pinacodera* Schaum, 1857; *Taridius* Chaudoir, 1875; *Pseudomasoreus* Desbrochers des Loges, 1904; and *Afrotarus* Jeannel, 1949. We have not seen material of *Assadecma* Basilewsky, 1982, so our comments about it are based on study of the description and illustrations. In spite of the rank accorded them, these taxa are not easily characterized on the basis of adult features. In our opinion, they are over-ranked. Accordingly, we make in the following pages adjustments in ranking that seem required by the evidence available.

We add to this subtribe a new monobasic genus, *Ceylonitarus*. Reasons for assigning this rank are presented below.

*Recognition.*— Diagnostic features of the subtribe are: head without suborbital setigerous punctures; elytron with penultimate umbilical puncture not laterad of antepenultimate and ultimate punctures; scutellar interneur separate from interneur 1, base of latter evident; tibiae average, spined laterally; tarsomeres slender, glabrous or setose dorsally, male front tarsomeres moderately expanded, articles 1-3 with biseriate adhesive vestiture ventrally; tarsal claws pectinate; ovipositor with stylomeres 1 and 2 subequal in length, stylomere 1 asetose; stylomere 2 without baso-dorsal projection, with one or two ensiform setae dorsally; preapical sensory furrow reduced, with one or two nematoid setae, or without these, and without furrow pegs;

mentum toothed, labial palpomere 2 bi- or plurisetose; apical margin of palpomere 3 subtruncate, or fusiform.

**Description.**—Standardized Body Length between 4.5 and 7.5 mm. Form slightly varied, from about average for Carabidae to somewhat flattened and broadened. Color mostly somber: dorsum rufous to black or metallic blue or green, appendages of most adults same color as that of dorsum, or paler; elytra either concolorous (adults of most species), or bicolored with various dark markings on paler background.

**Microsculpture.** Labrum and clypeus: with meshes isodiametric, microlines clearly visible at magnification of 50X. Frons and vertex with meshes isodiametric or microlines effaced. Pronotum with meshes isodiametric to transverse, or microlines effaced. Lateral and ventral sclerites of thorax with meshes transverse. Scutellum and elytra with meshes isodiametric to transverse, or effaced. Abdominal sterna with meshes transverse.

**Luster.** Dorsum various, dull to shining (most adults), to slightly iridescent.

**Standard or fixed setae.** Average for lebiines: head with two (or three) pairs of supraorbital setae; submentum and mentum each with single pair. Pronotum with two to six pairs of lateral setae, posterior pair near posterior angles. Prosternum with several setae at apex of intercoxal process. Elytra each with two or three discal setae, in interval 3; umbilical series continuous, 14 to 20 setae included, penultimate setigerous puncture not displaced laterally. Legs with average setation for carabids: tibia with full complement of spines; tarsomere 5 with row of spines on each ventro-lateral margin. Abdominal sterna with ambulatory setae, sternum VII with one or two pairs of setae in males, two pairs in females.

**Vestiture and surface.** Integument smooth, glabrous, or more or less densely to sparsely punctate, punctures with long or short slender setae; antennomeres 1-3 generally finely setose, or glabrous with apical ring of setae; tarsomeres dorsally glabrous or finely setose.

**Head.** About average in form for carabids. Frontal impressions shallow, broad. Clypeus average, transverse, about rectangular, anterior margins each slightly concave or truncate. Frons smooth, or rugulose (Fig. 50) laterally. Eyes average, moderately convex to reduced and flattened. Antennae filiform, antennomere 3 longer than 2 and 4, or subequal to latter articles; antennomeres each longer than wide, or width and length subequal and antenna shortened.

**Mouthparts.** Labrum like clypeus, in general form. Mandibles trigonal, average for carabids. Left mandible (Figs. 40.2A, B, 41A, B, 42A, B, 43A, B, 44A, B) with terebral margin well developed or reduced (most species), cutting edge retinacular ridge; posterior retinacular tooth small; premolar average, ventral surface with well developed premolar ridge; molar ridge present or absent; ventral groove average, setose throughout length, or absent. Right mandible (Figs. 40.2C, D, 41C, D - 44C, D) similar in overall size and form to left mandible; terebral margin well developed, tooth small or absent; retinacular ridge prominent or not, anterior retinacular tooth present or absent; premolar tooth present or absent, premolar ridge well developed; molar ridge present or absent. Maxilla average in form; lacinia (Fig. 45) extensively setose on ventral surface; galeomere 2 shorter than 1; palpomeres average, 4 fusiform, with apical margin subtruncate. Labium (Figs. 46-49) average; mentum with well developed tooth, broad or pointed apically, epilobes average; glossal sclerite broad, truncate and bisetose apically; paraglossae adnate to glossal sclerite, each paraglossa with short setae apically; palpomere 2 bi-, or plurisetose; palpomere 3 fusiform, with apical margin subtruncate, or in males expanded, securiform.

**Thorax.** Pronotum transverse, subcordate to subquadrate, surface slightly convex; basal margin beaded, subtruncate to distinctly lobed medially; anterior margin slightly concave; sides narrow to distinctly explanate; anterior angles broadly rounded; posterior angles acute to broadly rounded; median longitudinal impression distinct; posterior-lateral impressions shallow, indistinct. Prosternum with apex of intercoxal process immarginate. Pterothorax average, metepisternum elongate, with lateral margin greater in length than anterior margin; or subquadrate, with lateral and anterior margins subequal.

**Legs.** Average for Carabidae. Tarsomere 4 with apical margin subtruncate, not projected laterally as paired lobes; tarsal claws smooth or pectinate (Figs. 51-54), three to seven denticles per claw, denticles either sharp (adults of most species) or apices blunt. Male with front tarsomeres 1-3 (or 4) with adhesive vestiture ventrally; middle tarsomeres 1-4 without or with (adults of *Pinacodera*) adhesive vestiture.

**Elytra.** Average for lebiine adults: humeri broadly rounded (or sloped); apical margin subtruncate. Interneurs average, finely punctate or not; intervals flat to slightly convex.

**Wings.** Developed normally, or reduced to short stubs; species monomorphic or dimorphic for wing condition. Venation generally average for carabids: oblongum cell average (Figs. 73A, 74A, 84A, 85A); wedge cell (Figs. 73B, 74B, 84B, 85B) evident, though more or less reduced.

**Abdomen.** Abdominal sterna II-VII average for carabids, or sternum VII of males with posterior margin more or less deeply notched.

**Male genitalia.** Median lobe (Figs. 70-72; 86-88) cylindrical, anopic (Figs. 70-72) with apical orifice inclined to left and dorsal surface otherwise sclerotized; or catopic (Figs. 86-88) dorsal surface completely sclerotized; apical portion various, shorter or longer, narrow to very broad. Internal sac variously armored with vaguely defined fields of microtrichia, and with or without large, curved apical sclerite. Parameres average for lebiomorphs: left broad, about 0.33 length of median lobe; right short, but apex free, not fused to median lobe.

**Ovipositor and associated sclerites.** Tergum and sternum VIII average for lebiomorphs (as in Figs. 76A, B). Tergum X (Fig. 76C) with sclerotization reduced medially. Valvifer very broad and short. Stylomere 1 broad, slightly wider than long, asetose. Stylomere 2 (Figs. 55-61) as long or longer than stylomere 1, subcylindrical in form, without baso-dorsal

TABLE 2  
GEOGRAPHICAL DISTRIBUTION BY REGION, OF THE GENERA AND  
SUBGENERA OF CYMINDINA

NAME OF SUBGENUS	ZOOGEOGRAPHIC REGION				
	Afrotropical	Oriental	Palearctic	Nearctic	Neotropical
<i>Ceylonitarus</i>		x <sup>1</sup>			
<i>Cymindis</i> ( <i>s. lat.</i> )					
<i>Taridius</i>		x			
<i>Pinacodera</i>				x	x <sup>2</sup>
<i>Afrotarus</i>	x	x	x <sup>3</sup>		
<i>Cymindis</i> ( <i>s. str.</i> )		x	x	x	
<i>Hystrichopus</i> ( <i>s. lat.</i> )					
<i>Pseudomasoraeus</i>	x		x <sup>4</sup>		
<i>Assadecma</i>	x <sup>5</sup>				
<i>Hystrichopus</i> ( <i>s. str.</i> )	x				
<i>Plagiopyga</i>	x				
TOTALS	5	4	3	2	1

<sup>1</sup> Sri Lanka, only<sup>2</sup> Middle America, only<sup>3</sup> southern part of Arabian Peninsula, only<sup>4</sup> western Mediterranean basin, only<sup>5</sup> Madagascan, only

projection; ensiform setae one or two, longer (Fig. 55A) or shorter (Fig. 56A); trichoid setae few, ventral in position, or absent; preapical sensory furrow narrow, with one or two short nematoid setae or without these, and without furrow-peg setae; microsculpture (Figs. 62-65) almost isodiametric, more or less extensive; sculpticells with (Fig. 65) or without microspines.

**Classification.**— Eight genus-group taxa are arranged in two genera: *Cymindis* Latreille, and *Hystrichopus* Boheman. Taxa recognized by previous authors as subgenera of *Cymindis* are thus accorded lesser rank. Jeannel (1942a: 1039) also recognized within his subfamily Cyminditae two groups that correspond to the genera that we recognize: tribes Pseudomasoreini and Cymindini. At the time, however, he did not realize the close affinity between *Psuedomasoreus*, *Hystrichopus*, and *Plagiopyga*, and thus did not include the latter two groups in the Pseudomasoreini. A third genus is *Ceylonitarus*.

**Geographical distribution.**— This subtribe is basically Megagean in distribution, with one subgenus extending into the northern part of the Neotropical Region (*Pinacodera*; to Honduras, in Central America). Table 2 provides a summary. Details are presented below.

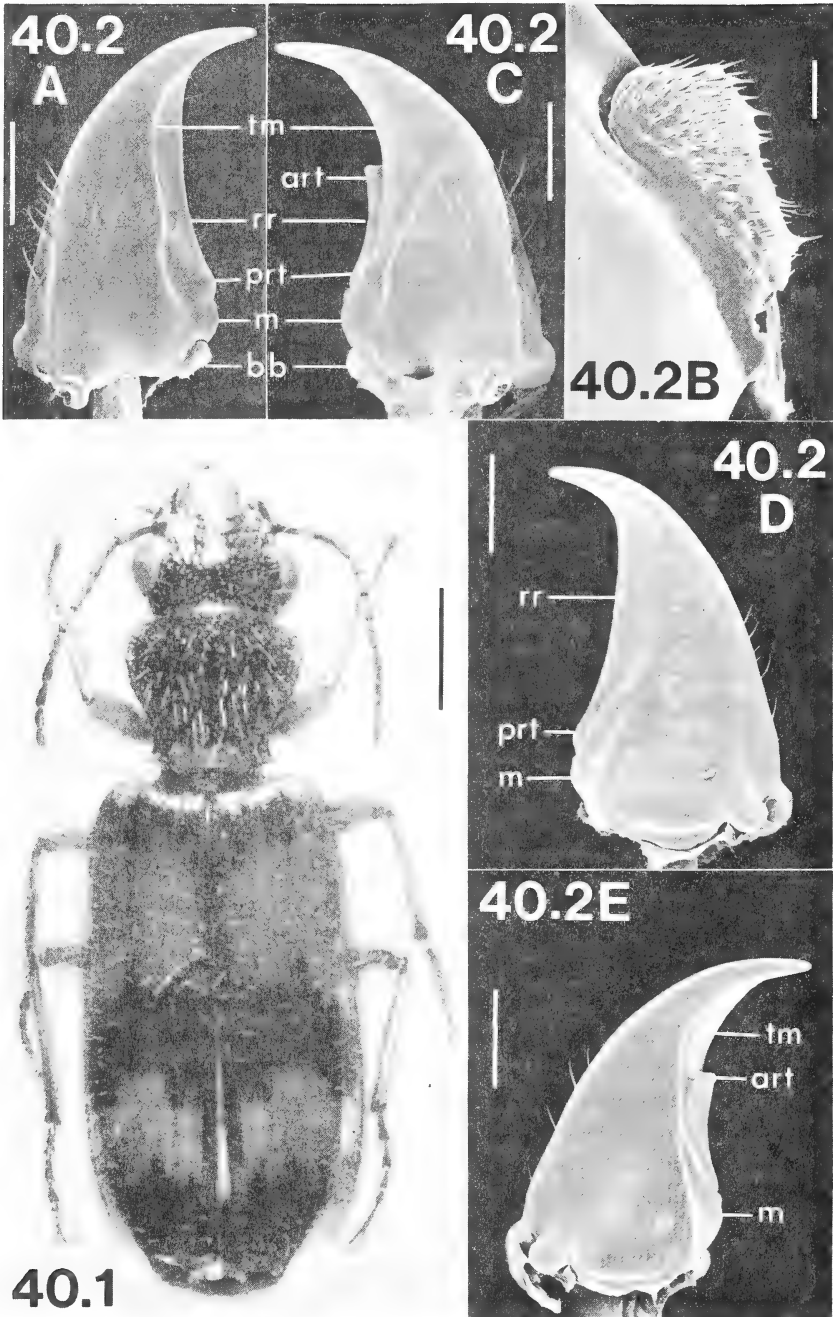
### Key to Genera and Subgenera of Cymindina

- 1 (0) Elytron with lateral umbilicate punctures not distinguishable from other serial setigerous punctures of intervals. Dorsum generally punctate and setose, serial setae of elytral intervals each more than half length of antennal scape. Head with three pairs of supraorbital setigerous punctures. Tarsal claws smooth, not pectinate. Elytra bicolored: flavous with black basal, medial, and apical fasciae (Fig. 40.1). Specimen from Oriental Region . . . *Ceylonitarus*, new genus, p. 135
- 1' Elytron with lateral umbilicate punctures distinctly larger than serial punctures of discal intervals. Dorsum various, glabrous or more or less setose. Head with two pairs of supraorbital setigerous punctures. Tarsal claws smooth or pectinate. Elytral color various. Specimen from Megagea, or from the northern Neotropical Region . . . . . 2.
- 2 (1') Specimen from locality in Nearctic or Neotropical Region . . . . . 3.
- 2' Specimen from locality in Palaearctic, Oriental, or Afrotropical Region . . . . 4.
- 3 (2) Dorsum glabrous or more or less densely setose. Male with tarsomeres 1-4 of both front and middle legs slightly widened, ventrally with adhesive vestiture *C. (Pinacodera)* Schaum, p. 149
- 3' Dorsum densely setose. Male with tarsomeres 1-3 of front legs only slightly widened, ventrally with adhesive vestiture . . . . . *C. (Cymindis)* Latreille(part), p. 156
- 4 (3') Dorsum with vestiture of short setae, more or less densely punctate, or at least intervals 4-7 each with several irregular rows of punctures; dorsal surfaces of tarsomeres sparsely to densely setose . . . . . 5.
- 4' Dorsal surface glabrous, elytral intervals impunctate, dorsal surfaces of tarsomeres sparsely setose or glabrous . . . . . 6.
- 5 (4) Frons with two sharply defined longitudinal ridges each side. Integument piceous; lateral margins of pronotum and elytra rufo-flavous. Pronotum with broad lateral margins. Range— Indian sub-continent, south of the Himalaya . . . . . *C. (Afrotarus)* Jeannel (part), p. 154
- 5' Frons laterally smooth, or with indistinct ridges. Integument various, of most specimens rufous or rufo-piceous, and elytra with or without pale marks.

Pronotum with lateral margins various. Range— Atlantic Islands, Africa north of Atlas Mountains, Palaearctic Region, including upper slopes of the Himalayan system . . . . .

- . . . . . *C. (Cymindis) Latreille*<sup>4</sup> (part) p. 156
- 6 (4') Frons laterally smooth or irregularly, sparsely punctate; without two or more regular ridges. Median lobe of male catopic (Fig. 86A). Stylomere 2 with single ensiform seta (Figs. 55A-57), in basal half . . . . . 7.
- 6' Frons each side with two or more regular ridges (Fig. 50). Median lobe of male anopic (Fig. 69A). Stylomere 2 of ovipositor with two ensiform setae, located in posterior half . . . . . 10.
- 7 (6) Mentum with pair of setae on tooth. Paraglossae glabrous. Antennomere 3 pubescent toward apex; internal sac of male genitalia with rows of small spines . . . . . *H. (Assadecma) Basilewsky*, p. 170
- 7' Mentum with setae on lateral lobes, only; paraglossae setose. Antennomere 3 pubescent toward apex, or nearly glabrous. Internal sac with or without spines 8.
- 8 (7') Antennomere 3 sparsely pubescent toward apex; denticles of tarsal claws sharp (Fig. 52); interval 3 of elytron with two or three setigerous punctures; stylomere 2 of ovipositor with moderate to long ensiform seta (Fig. 55A) . . . . . *H. (Pseudomasoreus) Desbrochers des Loges*, p. 158
- 8' Antennomere 3 not pubescent, with few long setae apically and preapically; tarsal claws smooth, or with sharp or blunt denticles; interval 3 of elytron with three or more setigerous punctures; stylomere 2 of ovipositor with ensiform seta very short (Figs. 56A and 57) . . . . . 9.
- 9 (8') Interval 3 of elytron with four or more setigerous punctures; tarsal claws with denticles sharp (as in Fig. 52) . . . . . *H. (Hystrichopus) Boheman*, p. 171
- 9' Interval 3 of elytron with two or three setigerous punctures; tarsal claws smooth, or with denticles blunt (Fig. 54) . . . . . *H. (Plagiopyga) Boheman*, p. 172
- 10 (6') Vertex and frons with isodiametric meshes; metepisternum with lateral margin distinctly longer than basal width, macropterous; pronotum with sides explanate; antennomeres 4-10 each distinctly longer than wide; internal sac of male genitalia (Fig. 69A) without large sclerite . . . . . *C. (Taridius) Chaudoir*, p. 145
- 10' Vertex and frons smooth medially, microlines effaced; metepisternum with lateral and basal margins subequal, brachypterous; sides of pronotum narrow; antennomeres 4-10 each 2.0 longer than wide, or shorter, not more than 1.5 longer than wide; internal sac of male genitalia (Figs. 70A, 71A) with large

<sup>4</sup>According to Antoine 1962: 567), adults of all species of subgenus *Cymindis* (as delimited here) have setose elytra, although in some species the setae are very short and sparse. In any event, glabrous- appearing specimens of subtribe Cymindina occurring to the north of the Pyrenees Mountains in Western Europe are members of subgenus *Cymindis*



Figs. 40.1-40.2. Photographs of *Cymindina*, *Ceylonitarus ceylonicus*, new species. Fig. 40.1: habitus, dorsal aspect (SBL = 5.92 mm.). ; Figs. 40.2A-E: SEM photographs of mandibles, A and D, left, dorsal and ventral aspects, respectively, B and E, right, ditto; C, basal brush of left mandible, dorsal aspect. Legend, mandibles: art, anterior retinacular tooth; bb, basal brush; m, molar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin. Scale bars = Figs. 40.1 = 1.0 mm.; Figs. 40.2A, C, D, and E = 200  $\mu$ m; Fig. 40.2B = 20  $\mu$ m.



sclerite .....  
 ..... *C. (Afrotarus) Jeannel* (part), p. 154

*Ceylonitarus* new genus

Figs. 40.1-40.6

GENERITYPE: *Ceylonitarus ceylonicus*, new species (here designated).

*Derivation of name.*— From the former name of the type area (“Ceylon”), and “*tarus*”, a name used in various combinations for *Cymindis*-like forms.

*Recognition.*— Diagnostic features of this taxon are: habitus *Cymindis*-like: color of elytra flavous, with three black fasciae (Fig. 40.1); body generally setose, setae long (Figs. 40.5A and B), head with three pairs of supraorbital setae; serial setigerous punctures of discal intervals of elytron as large as lateral umbilicate punctures, latter not readily distinguishable by eye; frons laterally shallowly and irregularly grooved; mandibles without ventral grooves (Figs. 40.2E and D), with large basal brushes (Fig. 40.2B); left mandible with well developed terebral margin (Fig. 40.2A); right mandible without premolar tooth (Figs. 40.2C and E); tarsal claws smooth; stylomere 2 of ovipositor narrow at base, falcate, with single long ensiform seta, dorso-lateral in position (Fig. 40.6A), ventral sensory furrow well removed from apex (Fig. 40.6B), without nematoid or furrow-peg setae, and microsculpture meshes of blade transverse, most sculpticells terminated apically with a microspine (Fig. 40.6C).

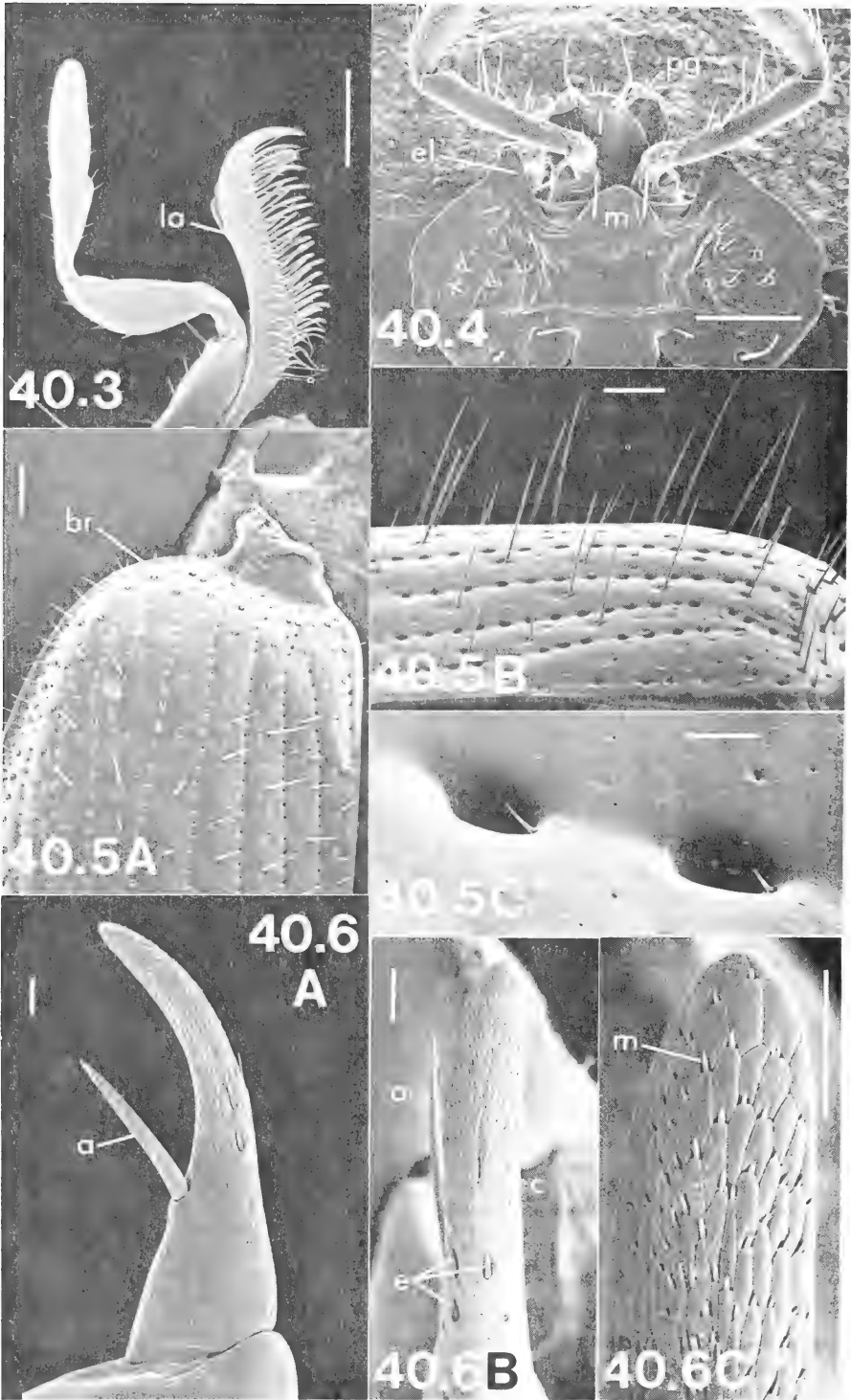
*Classification.*— Consideration in evolutionary terms of character states of *Ceylonitarus* compel us to rank this taxon as a genus, though we are reluctant to recognize monobasic genera. The following character states suggest that this group is more primitive than either *Cymindis* or *Hystrichopus*: left mandible with well developed terebral margin (Fig. 40.2A); maxilla with lacinia sparsely setose ventro-apically (Fig. 40.3; cf. Fig. 45); mental tooth not ridged (Fig. 40.4; cf. Figs. 46-49); terminal palpomeres narrow apically (Fig. 40.3; cf. Fig. 46); and stylomere 2 narrow and falcate. The extensive wedge cell of the wing is symplesiotypic for *Ceylonitarus* and *Hystrichopus*.

The following autapotypic features testify to the distinctness of the group: gains— an extra pair of supraorbital setae, additional antero-lateral marginal setae of pronotum, and the generally setose body; large basal brushes of the mandibles (Fig. 40.2B), and acute apices of lateral lobes of the mentum (Fig. 40.4); losses— ventral grooves, from mandibles; medial ensiform seta, nematoid setae, and furrow-peg setae, from stylomere 2.

The following apotypic features are shared with other cymindine taxa, but we believe they were acquired independently in each lineage: color pattern of elytra (shared with some members of subgenus *Taridius*); absence of microsculpture from most of dorsal surface, setose condition of body, and reduced basal ridge of elytron (shared with some members of *Cymindis sensu stricto*); stylomere 2 with single ensiform seta, dorso-lateral in position (shared with females of *Hystrichopus sensu lato*), and ensiform seta longer than usual (shared with females of subgenus *Pseudomasoreus*).

The smooth tarsal claws are difficult to interpret, for they may be primitively smooth, and thus plesiotypic, or secondarily smooth, and thus apotypic. In any event, this character state is shared with some members of the subgenus *Plagiopyga*.

The pattern of shared features suggests that they are examples of convergence, rather than of close relationship. Further, the plesiotypic features plus probably restricted geographical range that is peripheral to that of other cymindine groups, suggest to us that *Ceylonitarus* is a



Figs. 40.3-40.6. SEM photographs of structures of Cymindina, *Ceylonitarus ceylonicus*, new species.— Fig. 40.3: Right Maxilla, lacinia, palpifer, and palpus, ventral aspect. Fig. 40.4: Labium, ventral aspect, mentum and parts of prementum. Fig. 40.5: Left elytron—A, basal portion, dorsal aspect, B, basal portion dorso-medial aspect, c, two interneural punctures, dorso-medial aspect. Fig. 40.6: ovipositor, left stylomere 2—A, lateral aspect; B, ventral aspect; C, apical portion, ventral aspect. Legend, maxilla: la, lacinia. Legend, labium: el, epilobe; l, glo sal sclerite; m, mental tooth; pg, paraglossa. Legend, elytra: br, basal ridge. Legend, ovipositor, stylomere 2: a, lateral ensiform seta; c, sensory furrow; e, trichoid setae; m, microspine of sculpticell. Scale bars = Figs. 40.3-40.5B = 200  $\mu$ m; Figs. 40.5C-40.6C = 20  $\mu$ m.

phylogenetic relic, closer to the ancestral stock of the Cymindina than are the other two genera of this subtribe. The several and striking autapotypic features suggest the possibility of an extended period of isolation and probably of ethological (as well as structural) divergence from the other groups of cymindines.

Males are unknown. Features of the male genitalia might shed light on relationships of *Ceylonitarus*: if catopic, this would suggest close relationship with *Hystichopus*; if anopic, and with an elaborate apical sclerite on the internal sac, this would suggest close relationship with *Cymindis*. We believe that the median lobe will prove to be anopic, and the internal sac either devoid of armature, or with armature that is strikingly different from that of the taxa of *Cymindis*.

We think it possible that *Ceylonitarus* may include additional species. If so, the character states of such taxa might provide clues that will make possible a better assessment of the phylogenetic relationships of this group, and thus provide a better basis for its classification.

**Description.**— Size small (SBL less than 7.0 mm.), body slender, habitus as in Fig. 40.1. Color fuscous to flavous, with elytra markedly bicolored.

**Microsculpture.** Labrum with meshes isodiametric, sculpticells slightly convex. Rest of body surface without microlines (at least not visible at 50X; very faint vestiges on dorsum seen at 1000X), surface essentially smooth.

**Fixed setae.** Standard, except: head with three pairs of supraorbital setae; pronotum with several pairs of marginal setae in anterior 0.5. Abdominal sternum VII with four setae apically.

**Punctuation and vestiture.** Scape and antennomeres 2-4 generally setose, antennomeres 5-11 more densely so. Eyes glabrous. Head, prothorax, and lateral and ventral sclerites of pterothorax densely and moderately coarsely punctate, abdominal sterna more sparsely and finely so. Elytral interneurs more finely punctate than intervals; latter uniseriately punctate, setae flavous, many more than 0.5 length of antennal scape; serial punctures of discal intervals as large as umbilicate punctures, latter not readily distinguished by eye.

**Head.** Frons each side with two or three rather indistinct and irregular ridges. Frontal impressions shallow, indistinct. Eyes moderately prominent (Fig. 40.1). Antennae with antennomere 3 slightly longer than 4, but shorter than scape.

**Mouthparts.** Labrum larger than average ( $l/w$  0.59-0.68,  $\bar{x} > 0.62$ ). Mandibles as in Figs. 40.2A-E, both without premolar and ventral groove (Figs. 40.2D-E), and with large basal brush (Fig. 40.2B); left mandible with well developed terebral margin (Fig. 40.2A); right mandible with prominent retinacular ridge and small retinacular teeth (Figs. 40.2C and E). Maxillae average, lacinia ventrally with setae near medial margin, not extended to lateral margin pre-apically (Fig. 40.3), terminal palpomere fusiform, apex narrow. Labium (Fig. 40.4): mentum with lateral lobes acute apically; epilobes slender throughout, not toothed medially, and terminated at base of mental tooth; latter prominent, broadly rounded and immarginate apically; glossal sclerite broad, rounded apically; paraglossae membranous apically, setose, with apices extended slightly beyond plane of apex of glossal sclerite.

**Thorax.** Pronotum as in Fig. 40.1 (for details, see description of generitype). Ventral and lateral thoracic sclerites without notable features. Metepisternum with lateral margin clearly longer than basal margin.

**Elytra.** Dorsal surface deplanate. Base with humerus broadly rounded (Fig. 40.5A). Apical margin truncate and markedly sinuate. Basal ridge close to anterior margin, terminated near base of interval 5. Interneurs shallow, punctate. Epipleuron average.

**Wings.** Fully developed, veins rather pale and probably slightly sclerotized. Oblongum with short stalk (cf. Figs. 73A, 74A, and 84A), wedge cell more extensive than in *Cymindis* (cf. Figs. 73B and 74B).

**Legs.** Average for Cymindina, except tarsal claws smooth.

**Ovipositor.** Stylomere 1 glabrous, stylomeres 1 and 2 subequal in length. Stylomere 2 falcate in lateral aspect (Fig. 40.6A), slender, parallel-sided in ventral aspect, apex narrowly pointed. Lateral ensiform seta (Fig. 40.6A) longer than average, about half length of stylomere; several trichoid setae medio-ventrally. Following setae lacking: medial ensiform, nematoid, and furrow-peg. Sensory furrow (Fig. 40.6B) very narrow, about half way between apex and plane of insertion point of ensiform seta. Microsculpture: meshes generally transverse, broadly so basally (Fig. 40.6A), more narrowly so preapically (Figs. 40.6B and C); sculpticells flat basally, convex preapically, though not keeled, most terminated with single microspine (Fig. 40.6C).

**Relationships of genus.**— We believe that *Ceylonitarus* is more primitive than *Cymindis* or *Hystichopus*, and is the sister group of the ancestral stock of these two genera. See "Classification", above, for a discussion of the basis for this hypothesis.

**Included species.**— Only one, *C. ceylonicus*, new species, described below.

*Ceylonitarus ceylonicus*, new species

**Type material.**— HOLOTYPE female, labelled: SRI LANKA Man. Dist. 8 mi. SE Mannar black light 15 feet, 6 Nov. 1976; Collected by G. F. Hevel, R. E. Dietz IV, S. Karunaratne, D. W. Balasooriya (USNM). Seven paratypes, females, labelled: SRI LANKA Man. Dist. 4 mi. NW Mannar black light, 100 ft. 3 November 1976; collector label same as for holotype (USNM). TYPE LOCALITY: vicinity of Mannar, Sri Lanka.

**Derivation of specific epithet.**— From the former name of the type area, Ceylon.

**Recognition.**— Color pattern (Fig. 40.1) of adults of this species is like that of the mainland species *Cymindis* (*Taridius*) *stevensi*, known from the Nilgiri Hills of India. The two are easily distinguished, however, by differences in: setation (adults of *C. stevensi* with dorsal integument glabrous except for normal fixed setae; adults of *C. ceylonicus* with dorsal integument generally setose); microsculpture (pronotum and elytra of *C. stevensi* with meshes distinct; these surfaces smooth in *C. ceylonicus*); details of color pattern of elytra (cf. Figs. 40.1 and 75B); pronotum (sides explanate in *C. stevensi* adults, not so in members of *C. ceylonicus*); tarsal claws (pectinate in *C. stevensi*; smooth in *C. ceylonicus*); and in setae of stylomere 2 (*C. stevensi* females with median and lateral ensiforms, nematoids, and furrow-pegs; *C. ceylonicus* females with only lateral ensiform).

**Description.**— Habitus as in Fig. 40.1, *Cymindis*-like. Standardized Body Length 5.36-6.64 mm. ( $\bar{x}=6.02$  mm).

Color. Head and pronotum dorsally rufo-piceous to piceous, rufous ventrally. Elytra with disc predominantly flavous, with suture dark, and three black fasciae (Fig. 40.1); epipleura flavous. Metepisterna and abdominal sterna rufo-piceous, other sclerites of pterothorax rufous; antennae, palpi, and legs flavous.

Microsculpture, setation, form of head, details of mouthparts, thorax (except pronotum), elytra, legs, abdominal sterna and ovipositor sclerites as described for genus, above.

Pronotum. As wide as or slightly wider than head (Hw/Pwm 0.93-1.00,  $\bar{x}=0.96$ ), slightly wider than long (Pl/Pwm 0.83-0.91,  $\bar{x}=0.87$ ), width near mid-line greater than width at base (PwB/Pwm 0.67-0.73,  $\bar{x}=0.71$ ). Sides narrow, not explanate, sharply beaded, markedly sinuate. Anterior lateral angles broadly rounded; posterior-lateral angles rectangular or acute, distinctly anterior to medial part of basal margin. Basal margin not beaded, laterally with short, marked sinuation. Disc markedly convex medially, sloped downward laterally. Marginal grooves narrow, continuous with narrow posterior-lateral impressions. Median longitudinal impression shallow; anterior transverse impression indistinct; posterior transverse impression broad, shallow, continuous with posterior-lateral impressions.

**Geographical distribution.**— Known only from low altitude localities, in the vicinity of Mannar, Sri Lanka, where the specimens were taken at light.

**Material examined.**— Type series, only. We owe a special note of thanks to Terry Erwin, who drew these specimens to our attention, and made them available for our study.

*Cymindis* Latreille

Figs. 41-43, 45-51, 53, 59-63, 65, and 67-76

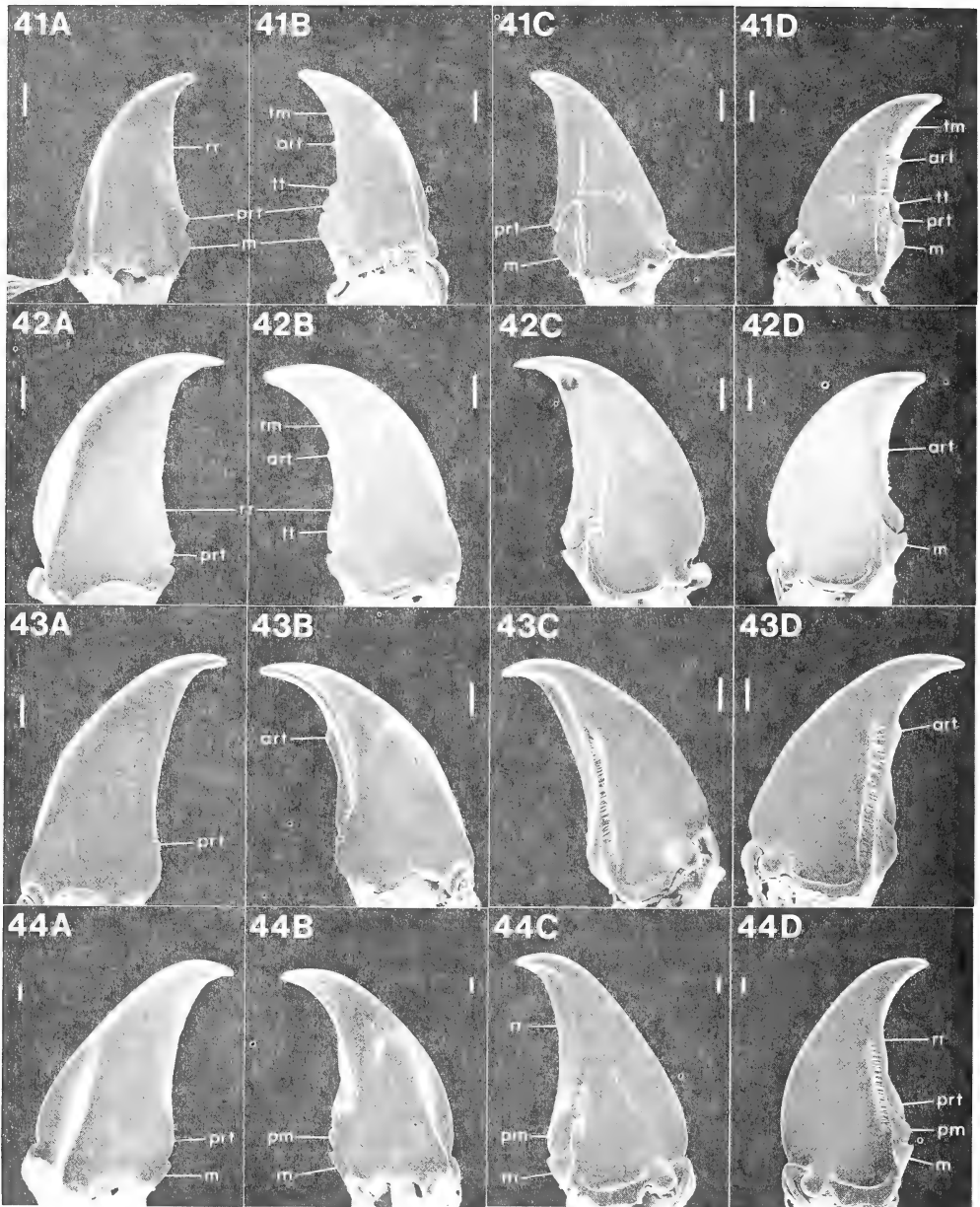
*Cymindis* Latreille, 1806: 190. GENERITYPE: *Buprestis humeralis* Fourcroy, 1785:57 (monotypy).— Chaudoir, 1873: 53-120.— Csiki, 1932:—. Jeannel, 1942a: 1041-1056.— Antoine, 1962: 564-587.— Jedlička, 1963: 452-461.— Habu, 1967: 57-74.— Lindroth, 1969: 1070-1086.— Ball, 1982:—.

*Pinacodera* Schaum, 1857: 294. GENERITYPE: *Cymindis limbata* Dejean, 1831:320 (designated by Lindroth, 1969: 1067).— LeConte, 1861: 24.— Chaudoir, 1875: 2.— Horn, 1881: 156.— 1882: 146.— LeConte and Horn 1883: 45.— Bates, 1883: 187-188.— 1884: 296.— Blatchley, 1910: 142, 152.— Leng, 1920: 67.— Casey, 1920: 279.— Csiki, 1932: 1487.— Blackwelder, 1944: 62.— Jeannel, 1949: 878.— Ball, 1960: 161.— Lindroth, 1969: 1067-1070. Erwin *et al.*, 1977: 4.58.— Ball, 1982:—, NEW SYNONYMY.

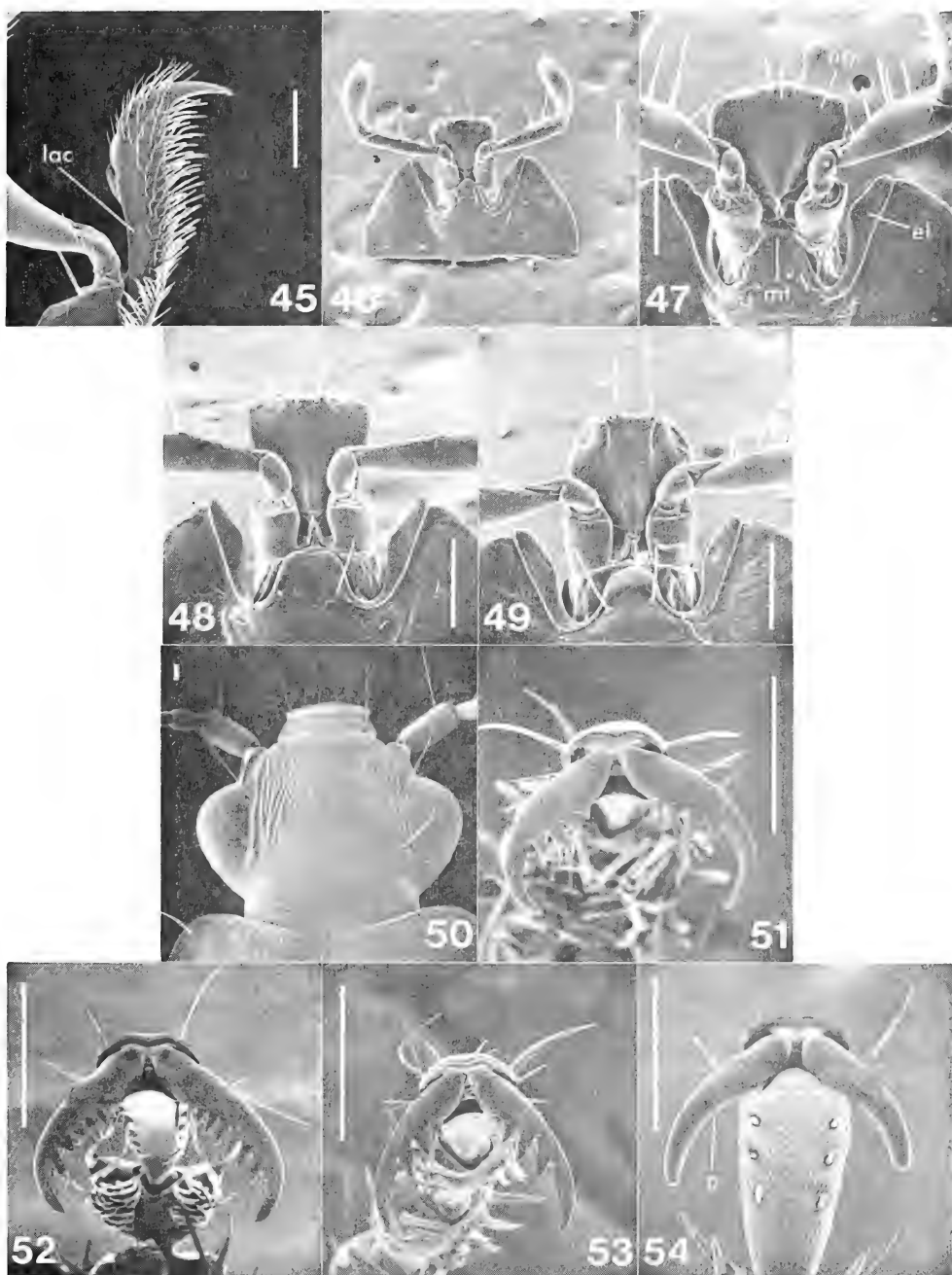
*Planesus* Motschulsky, 1864: 240(table). GENERITYPE: *Cymindis fuscata* Dejean, 1831:321 (= *Cymindis platicollis* Say, 1823) (original designation by Motschulsky, 1864: 240 (table)).

*Taridius* Chaudoir, 1875: 71. GENERITYPE: *Taridius opaculus* Chaudoir, 1875: 7 (monotypy).— Bates, 1892: 416).— Andrewes, 1930: 342-343.— Csiki, 1932: 1489.— Andrewes, 1935: 204-205.— van Emden, 1937: 123-125.— Jedlička, 1963: 461.— Ball, 1982:—, NEW SYNONYMY.

*Afrotarus* Jeannel, 1949: 878. GENERITYPE: *Cymindis kilimana* Kolbe, 1898: 51 (original designation).— Basilewsky, 1962: 252.— 1968a: 360.— Ball, 1982:—, NEW SYNONYMY

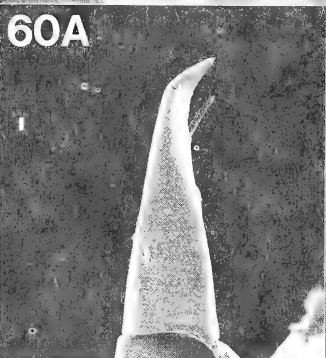
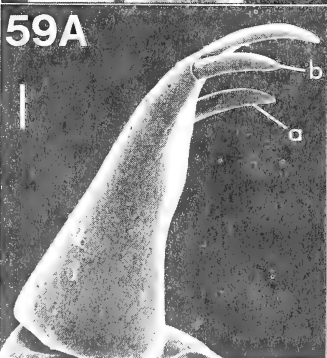
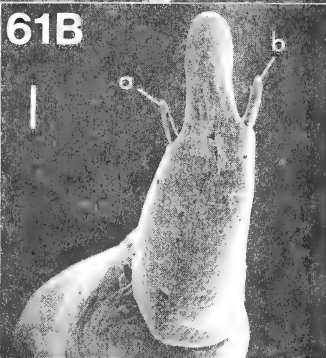
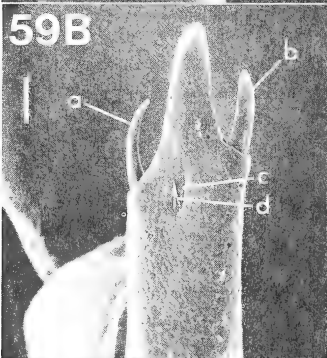
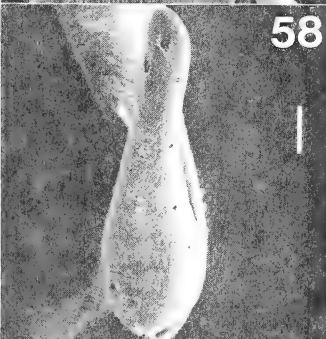
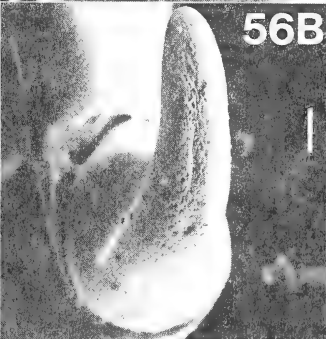
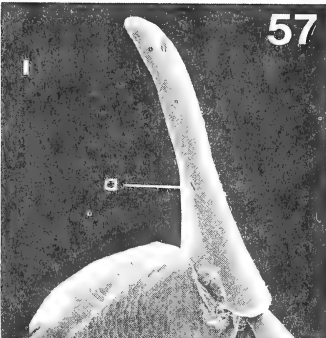
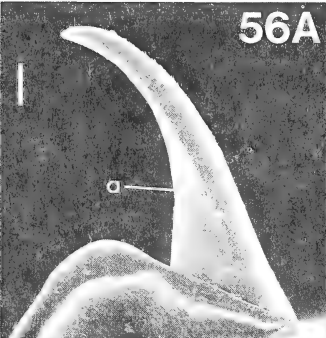
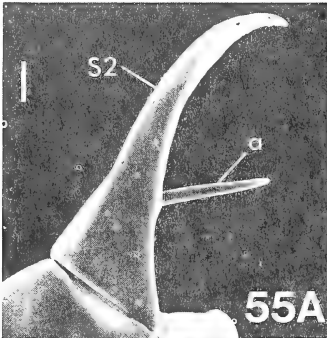


Figs. 41–44. SEM photographs of structures of Cymindina.—Mandibles —A and C, left, dorsal and ventral aspects, respectively, B and D, right, dorsal and ventral aspects, respectively.— 41, *Cymindis (sensu stricto) suturalis* Dejean; 42, *C. (Taridius) opacula* (Chaudoir); 43, *C. (Pinacodera)* new species no. 1; 44, *Hystrichopus (sensu stricto)* near *dorsalis* Thunberg. Scale bars = 100  $\mu$ m. Legend: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tm, terebral margin; tt, terebral tooth; vg, ventral groove.



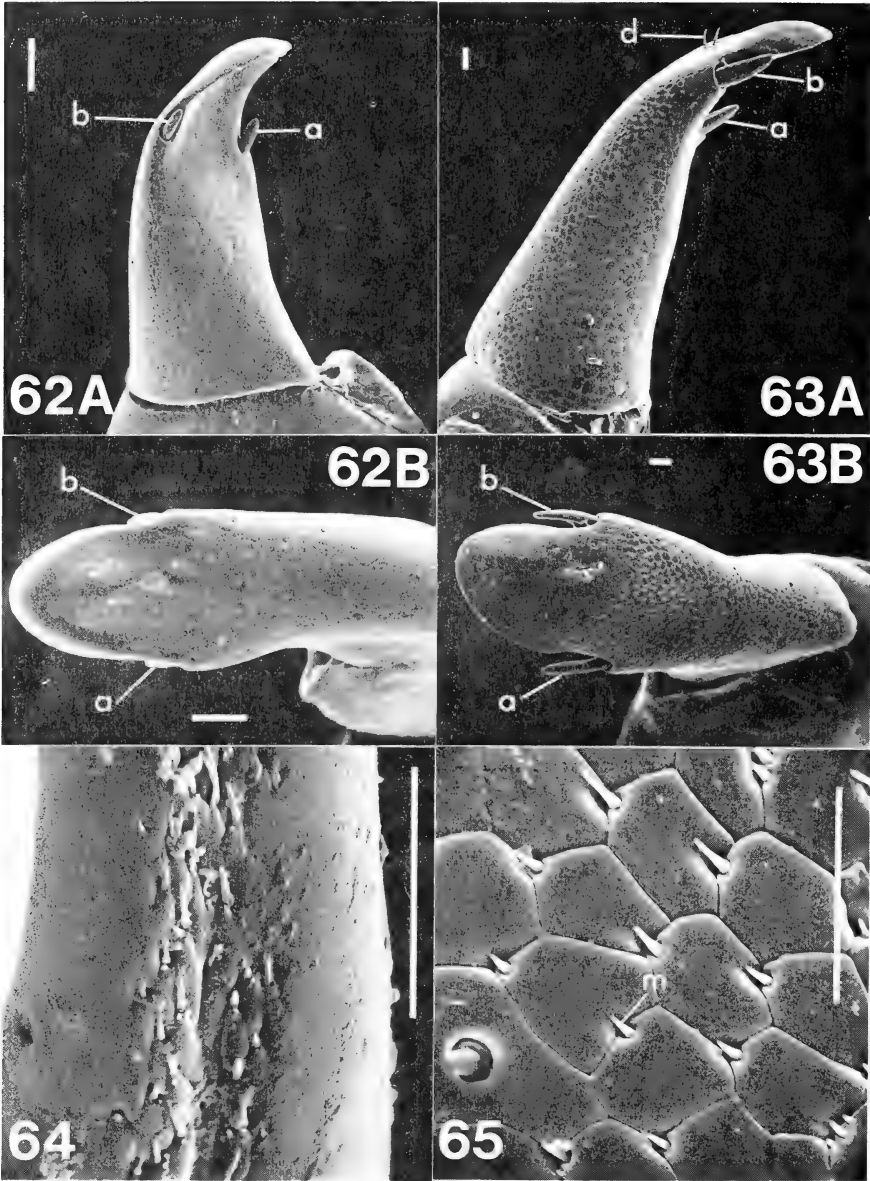
Figs. 45–54. SEM photographs of structures of Cymindina. Mouthparts and tarsal claws. Fig. 45: *C. (Pinacodera) limbata* Dejean, right maxilla, ventral aspect. Figs. 46–49, labium, ventral aspect: 46, *C. (P.) limbata*; 47, *C. (P.)* new species no 2; 48, *C. (P.)* new species no. 1; 49, *C. (Taridius) opacula*. Fig. 50: *C. (Taridius) opacula*, head, dorsal aspect. Figs. 51–54, tarsal claws, terminal aspect: 51, *C. (T.) opacula*; 52, *Hystrichopus (sensu stricto) nr. dorsalis*; 53, *C. (Afrotarus) kilimana* Kolbe; 54, *H. (Plagiopyga) cymindoides* (Péringuey). Scale bars = 200  $\mu$ m. Legend, labium: el, epilobe of mentum; l, glossal (or ligular) sclerite; m, tooth of mentum; pg, paraglossa. Legend, tarsus: p, denticle of tarsal claw.







Figs. 55–61. SEM photographs of structures of Cymindina.—Left stylomeres of ovipositor. Fig. 55: *Hystrichopus (Pseudomasoreus) capicola* Basilewsky, A and B, medial and ventral aspects, respectively. Fig. 56: *H. (sensu stricto) nr. dorsalis* Thunberg, A and B, lateral and ventral aspects, respectively. Figs. 57, 58: *H. (Plagiopyga) cymindoides* (Péringuey), lateral and ventral aspects, respectively. Figs. 59–61, A and B, medial and ventral aspects, respectively: 59, *Cymindis (Afrotarus) kilimana* Kolbe; 60, *C. (Taridius) opacula* (Chaudoir); 61, *C. (sensu stricto) hieronticus* (Reiche). Scale bars = 20  $\mu$ m. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow; d, nematoid seta; S2, stylomere 2.



Figs. 62–65. SEM photographs of structures of Cymindina.—Ovipositor, left stylomere 2. Figs. 62–63, A and B, medial and ventral aspects, respectively: 62 *Cymindis (sensu stricto) suturalis* Dejean; 63, *C. (Pinacodera)* new species no. 1. Figs. 64 and 65, microsculpture: 64, *Hystrichopus (sensu stricto)* nr. *dorsalis* Thunberg; 65, *C. (P.)* new species no. 1. Scale bars = 20 μm.

*Recognition.*— Diagnostic features of this genus are the following: head with two pairs of supraorbital punctures; frons with (most members) or without longitudinal ridges and grooves laterally; elytron with lateral umbilicate punctures larger than, and thus clearly distinguishable from, setigerous punctures of discal intervals; right mandible without premolar tooth; median lobe of male genitalia anopic, internal sac with or without sclerites; stylomere 2 of ovipositor broad at base, with two ensiform setae on dorsal margins.

*Classification.*— Although the four groups ranked as subgenera are not easy to diagnose for recognition of individual specimens, we are satisfied that each is monophyletic, and is reasonably distinctive in combinations of structural features, and in patterns of geographical distribution. The sequence of subgenera in the text is based on our concept of sister-group relations, as discussed in more detail, below.

The characteristic form of stylomere 2 of the ovipositor (relatively straight, broad at least preapically in ventral aspect), with ensiform setae relatively close to the apex (Figs. 59-62) seems to be apotypic, and is the only such feature for delimiting *Cymindis* (*sensu lato*) in relation to *Hystrichopus* (*sensu lato*). It is sufficient, however, to suggest that *Cymindis* is monophyletic.

Features interpreted as synapotypic for *Cymindis* (*sensu lato*) and *Hystrichopus* (*sensu lato*) and that thus support inference of a sister group relationship for these two taxa are the ridged mental tooth (Figs. 46-49), and pectinate tarsal claws (Figs. 51-54; denticles reduced in some members of subgenus *Plagiopyga*, and interpreted as lost from other members).

#### Subgenus *Taridius* Chaudoir, new status

Figs. 42, 49-51, 60, 69, 73, and 75

*Diagnostic description.*— Size small (SBL ca. 5.5-7.4 mm.) to average (ca. 10 mm.). Color: uniformly rufo-piceous to piceous, or elytra bicolored piceous and flavous (Figs. 75A, B) appendages paler (rufous or flavous) than dorsum. Microsculpture: head— vertex and frons with meshes isodiametric, lines clearly developed; pronotum with meshes transverse; elytra— dorsal surface with meshes isodiametric. Vestiture: dorsum glabrous, except for standard setae, dorsal surfaces of tarsomeres each with single pair of setae near apex, or very sparsely setose (*i.e.*, one or two additional short setae). Head: frons each side with from two to seven (Fig. 50) sharply defined ridges. Antennae: scape and antennomeres 2 and 3 with ring of setae near apex, otherwise glabrous; antennomeres 4-11 generally setose; antennomeres 3 and 4 subequal in length. Mandibles as in Figs. 42A - D. Labium as in Fig. 49. Metepisternum with lateral margin clearly longer than anterior margin. Wings fully developed, oblongum and wedge cells as in Figs. 73A and B. Tarsal claws as in Fig. 51. Median lobe of male genitalia (Figs. 69A, B) with apex simple; internal sac without sclerotized plate. Stylomere 2 of ovipositor average for cymindoids, though more slender apically than in *Pinacodera* (Fig. 60A; cf Fig. 63A); microspines on ventral surface.

*Relationships of subgenus.*— Compared to other subgenera of *Cymindis*, *Taridius* seems more primitive, and thus likely to be the sister group of *Pinacodera* - *Afrotarus* - *Cymindis*. Adults share with those of *Pinacodera* and some adults of *Cymindis* similar body form and fully developed wings—but these features are correlated functionally and symplesiotypic. Females of *Taridius* and *Pinacodera* share microspines on stylomere 2 (Figs. 60B and 65). However, females of *Ceylonitarus* and *Hystrichopus* (*sensu stricto*) also exhibit this feature (Fig. 64), and so we are disinclined to weight it heavily, for the similarity might be symplesiotypic or homoplasious. In fact, *Taridius* seems to be without autapotypic character states, and thus may be paraphyletic.

The distribution pattern is consistent with a relict status for *Taridius*: populations of this structurally plesiotypic group occupy montane areas which are marginal relative to lowland tropical forests. This suggests displacement from the surrounding lowland tropics. However, it is also possible that the species are persisting in those areas where forest is still able to persist;

thus, the distribution pattern is the result of recent ecological circumstances, rather than temporally remote events.

*Included species.*— Three species are recognized: *C. opacula* (Chaudoir, 1875); *C. birmanica* (Bates, 1892); and *C. stevensi* (Andrewes, 1923). The first two species are each monobasic. *C. stevensi* includes three subspecies: *C. s. stevensi*; *C. s. nilgirica* (Andrewes, 1935); and *C. s. andrewesi* (van Emden, 1937). Adults of these species and subspecies are distinguished from one another in the following key. Andrewes (1935: 204-205) also included in *Taridius*, *C. nigra*, but adults of this taxon have features of *Afrotarus* Jeannel, a group with which Andrewes was unfamiliar when he published his treatment. At that time, *Afrotarus* had not been erected, only two of its species had been described (in *Cymindis*), and they were known only from the high mountains of East Africa and Abyssinia. Thus, Andrewes could not be expected to be aware of the true affinities of his new species from the highlands of South India.

*Notes about habitat.*— Andrewes (1935: 205) recorded that type material of *C. s. nilgirica* was collected among dead leaves at 6000 feet above sea level, in the Nilgiri Hills.

*Geographical distribution.*— The species of this subgenus are known from the Palni and Nilgiri Hills of South India, and from the hills of northeastern India, western Burma, and eastern Java. Andrewes (1930: 343) lists localities.

*Relationships of the species.*— These are not clear. *C. opacula* and *C. birmanica* are synapotypic in sculpture of the dorsum of the head, whereas *C. birmanica* and *C. stevensi* are synapotypic in color pattern. One of these discordant pairs of synapotypies is homoplasious, but we are not in position to infer which.

#### Key to Species of Subgenus *Taridius* Chaudoir

- 1 (0) Pronotum with more than two pairs of lateral setae; dorsum concolorous, rufo-piceous ..... *C. (Taridius) opacula* (Chaudoir), p. 147
- 1' Pronotum with two pairs of lateral setae; dorsum bicolored: each elytron predominantly flavous, with piceous or black longitudinal marks suturally, marginally, and transversely in posterior 0.33 (Figs. 75A, B) ..... 2.
- 2 (1') Frons each side with at least five longitudinal carinae (cf. Fig. 50) ..... *C. (Taridius) birmanica* (Bates), p. 147
- 2' Frons with not more than three longitudinal carinae each side ..... 3.
- 3 (2') Pronotum narrow (Hw/Pmw 0.82-0.86), flavous color extended from margins to larger areas of disc, or confined to reflexed margins; elytron with transverse dark mark interrupted or very narrow (Fig. 75A) ..... *C. (Taridius) s. andrewesi* (van Emden).
- 3' Pronotum broad (Hw/Pmw 0.73-0.80), with only reflexed margins flavous, otherwise piceous; elytron with transverse dark mark various ..... 4.
- 4 (3') Elytron with transverse dark mark continuous, broad medially (Fig. 75B) ..... *C. (Taridius) s. nilgirica* Andrewes).
- 4' Elytron with transverse dark mark interrupted or very narrow medially (Fig. 75A) ..... *C. (Taridius) s. stevensi* (*sensu stricto*), p. 147

*Cymindis (Taridius) opacula* (Chaudoir) NEW COMBINATION

Figs. 42A-D, 50-51, and 60A, B

*Taridius opaculus* Chaudoir, 1875: 8. TYPE AREA.—“le nord de l’Hindostan”.—Bates, 1892: 152.—Iakobson, 1907: 396.—Csiki, 1932: 1489.—Andrewes, 1935: 204.—Jedlička, 1963: 462. Not seen.

**Geographical distribution.**—This species is known from northern India and northern Burma, within the range of, but generally at lower elevations than, *C. stevensi*.

**Material examined.**—Two males, four females, Assam Lohara Kaziranga 110 m. X.7-16.61 E. S. Ross, D. Q. Cavagnaro (CAS). Female, Calcutta (IRSB).

*Cymindis (Taridius) birmanica* (Bates) NEW COMBINATION

*Taridius birmanicus* Bates, 1892: 152. TYPE LOCALITY: Teinzo, Karin Cheba, 1300-1400 m.—Andrewes, 1930: 343.—Csiki, 1932: 1489.—Andrewes, 1935: 204.—Jedlička, 1963: 462.

**Geographical distribution.**—This species is known only from the Karen Hills of western Burma. We have not seen any specimens.

**Notes.**—To judge from the original description, the type specimens of this species have the flavous marks of the elytra smaller than is characteristic of specimens of *C. stevensi*.

*Cymindis (Taridius) stevensi* (Andrewes), NEW COMBINATION

Figs. 75A, B

*Taridius stevensi* Andrewes, 1923: 689. CO-TYPE labelled: Cotype [circular label, ringed with green]; Gopaldhara, Darjeeling H. Stevens 1919; H. E. Andrewes coll. BM 1945-97; *Taridius Stevensi* Andr. cotype H. E. Andrewes det. [handwritten]. (BMNH). TYPE LOCALITY: Sikkim, Golpadhara (near Darjeeling).—Andrewes, 1930: 343.—Csiki, 1932: 1489.—Andrewes, 1935: 204.

*Taridius nilgiricus* Andrewes, 1935: 204. LECTOTYPE (here selected) female, labelled: Cotype [circular label, ringed with green]; Nilgiri Hills H. E. Andrewes; *Taridius nilgiricus* co-type Andr. H. E. Andrewes det. [handwritten] (BMNH). TYPE LOCALITY: Nilgiri Hills, India. NEW SYNONYMY.

*Taridius andrewesi* van Emden, 1937: 123. TYPE LOCALITY: Java, Tengger, Nonkodjadjan. NEW SYNONYMY.

**Notes about synonymy.**—The specimens included by us in *C. stevensi* (*sensu lato*) represent three nominal species. They are combined on the basis that differences are slight and diagnostic characters sufficiently variable to suggest at most a pattern of step-clines. One of the principal diagnostic features claimed by Andrewes for *C. nilgirica* is extra setae on elytral intervals 3 and 5. However, the elytra of the lectotype are asymmetric in number of setae, and the other specimens from the Nilgiri Hills have the normal number of two setigerous punctures in interval 3. Thus, the lectotype is interpreted as simply an abnormal specimen.

Van Emden (1937: 123) provided a detailed description of *C. andrewesi*, but the only differences that seem of diagnostic value are given above, in the key.

**Pattern of variation.**—Two discordant clines are suggested: decrease in amount of black pigment of the elytra from southern to northern India; and decreased width of the pronotum from northeastern India to western Burma (expressed as increase in value for Hw/Pmw- Table 3). In color pattern, adults of *C. s. stevensi* are more like those of *C. s. andrewesi*, whereas in proportions of the pronotum, *C. s. stevensi* is more like *C. s. nilgirica*.

**Geographical distribution.**—*Cymindis s. nilgirica* is known only from the Western Ghats of southern India (Nilgiri and Palni Hills). *C. s. stevensi* ranges along the lower southern slopes of the Himalaya from Sikkim to Haldwani in the United Provinces, and in the Kondmal Hills of the Eastern Ghats (Andrewes, 1923: 690). Before central India was cleared in historic times of its forests (Dilger, 1952: 125-127), it seems possible that the ranges of *C. s. stevensi* and *C. s. nilgirica* were in contact.

TABLE 3  
DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (MM) AND IN  
VALUES FOR THE RATIO Hw/Pmw AMONG SAMPLES OF *CYMINDIS STEVENSI*  
(ANDREWES)

SUPSPECIES AND LOCALITY	N	SBL RANGE	MEAN	Hw/Pmw RANGE	MEAN
<i>C. s. nilgirica</i>					
Palni Hills	1 ♀	7.32		0.74	
Nilgiri Hills	3 ♀	5.84–6.90	6.22	0.79–0.80	0.79
<i>C. s. stevensi</i>					
Sikkim	1 ♀	6.42		0.77	
Gopaldhara	2 ♀	6.40–6.90	6.65	0.73–0.78	0.76
	1 ♂	5.80		0.76	
<i>C. s. andrewesi</i>					
Karen Hills, Burma	1 ♀	6.78		0.82	
Java	1 ♂	6.48		0.83	
	1 ♀	5.80		0.86	

*Cymindis s. andrewesi* occupies areas to the east of the Irawaddy River, with samples known from as far north and west as the Karen Hills of Burma and as far south and east as the Indo-Australian island of Java.

*Chorological affinities.*— The range of *C. s. stevensi* is overlapped by that of *C. opacula*, though the two species have not been recorded from the same locality. The range of *C. s. andrewesi* overlaps that of *C. birmanica* in the Karen Hills. Locality data are not sufficiently precise to indicate if the two taxa are microsympatric, or if their life cycles are synchronic. Nonetheless, these geographical contacts are reasonable evidence for reproductive isolation between *C. stevensi* and the other two species. Specific distinctness of *C. opacula* and *C. birmanica* is not tested by chorological data.

*Material examined.*— In addition to type material recorded above, we have seen nine specimens, as follows.

*C. s. nilgirica.* Three females: Nilgiri Hills, H. E. Andrewes (BMNH); same locality, collected by G. F. Hampson (BMNH); and Palni Hills, Kodaikanal, 6900–7200 ft., IZ. 22, S. Kemp (ZSIC).

*C. s. stevensi.* Male and three females (including one paratype) Gopaldhara, Darjeeling, Sikkim, H. Stevens (BMNH).

*C. s. andrewesi.* Male, female, paratypes, O. Java Tengger Nonkodjadjan 1300 m. Wegner (BMNH). Female, Burma Karen Hills; Taridius sp. H. E. Andrewes det. (BMNH).

Subgenus *Pinacodera* Schaum, new status

Figs. 43, 46-48, 63, 65, and 76

**Diagnostic description.**— Body moderately flattened, generally elongate. Size about average for carabids, SBL ca. 5.50-10.50 mm. Color: somber, with dorsum of most specimens darker than venter, and appendages paler than body integument; head rufous, piceous or black; pronotum rufous, piceous, or black, lateral areas paler or not, than disc; elytra with dorsal surface rufo-flavous, rufous, piceous, or black, or various combinations of these, epipleura of most specimens paler than dorsal surface; venter rufous, piceous, or black; antennae rufo-flavous, or rufo-piceous, with scape of most specimens paler than remaining antennomeres; legs rufo-flavous to black, with femora of most specimens paler than other articles. Microsculpture: meshes in general, isodiametric, or transverse, but comparatively wide; head— frons and clypeus with meshes isodiametric, microlines distinct or indistinct, or meshes partially or wholly effaced, ventral surface with meshes transverse, microlines clear, or partially or wholly effaced; pronotum with meshes uniformly transverse, or isodiametric postero-laterally, lines clear or partially or wholly effaced; scutellum and elytra with meshes uniformly isodiametric; prosternum and pterothorax ventrally with meshes transverse, microlines clear, or partially or wholly effaced, proepisternum with meshes oblique, microlines partially or wholly effaced; abdominal sterna with meshes transverse, microlines clear or partially or wholly effaced. Vestiture: glabrous (except fixed setae), or sparsely to densely setose and punctate; elytral intervals impunctate, or with one or more irregular rows of setigerous punctures. Head: frons each side with two to five irregular longitudinal ridges and grooves more or less distinctly developed. Antennomeres 1-3 either glabrous (except normal preapical setae) or sparsely setose, setae short; antennomeres 3 and 4 subequal in length. Mandibles as in Figs. 43A-D. Lacinia as in Fig. 45. Labium as in Figs. 46-48. Metepisternum either distinctly longer than wide, or width at base and length of lateral margin subequal. Wings fully developed, or reduced to short stubs. Median lobe of male genitalia with apical portion in lateral aspect straight and narrow, or expanded slightly into knob, internal sac with sclerotized plate, as in subgenus *Cymindis* (cf. Fig. 72C), or without armature. Stylomere 2 of ovipositor average for *Cymindis* (Figs. 63A, B; cf. Figs. 62A, B); microspines on ventral surface (Fig. 65).

**Included species.**— Twenty seven species are known of which nine are described. The group is presently under study by us.

**Way of life.**— Data about life histories are available for two species, *C. platicollis* Say, and *C. limbata* Dejean (Mahar, 1978). Adults of both species are crepuscular or nocturnal, living on ground in leaf litter, and in trees. Larvae are terrestrial. *C. platicollis* is a spring breeder, while *C. limbata* breeds during summer. Site of oviposition has not been determined.

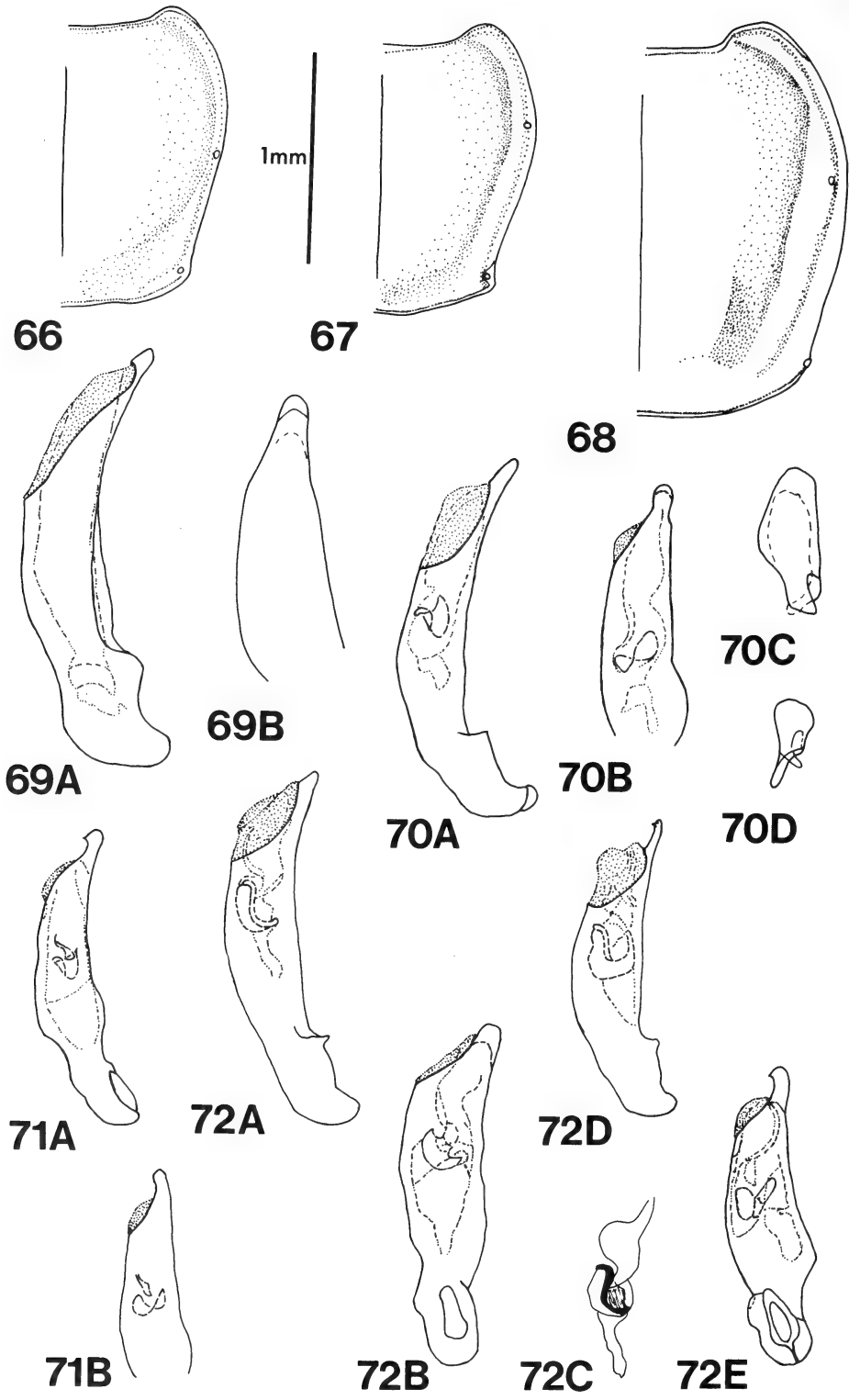
**Notes about habitat.**— Taxa are associated with arboresecent vegetation, from desert, tropical thorn scrub and thorn forest, to dry oak forests, wet conifer forests and cloud forests in the mountains of northern Middle America. Altitudinal range of the subgenus extends from sea level to 2900 meters above sea level.

**Geographical distribution.**— The range of this subgenus extends from Honduras in Middle America, to southern Nova Scotia and Ontario, in eastern North America.

**Classification.**— The species are arrayed in two groups: a more northern group, males of which have armature in the internal sac, and a more southern group whose males have unarmored internal sacs.

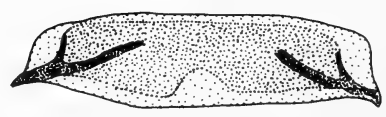
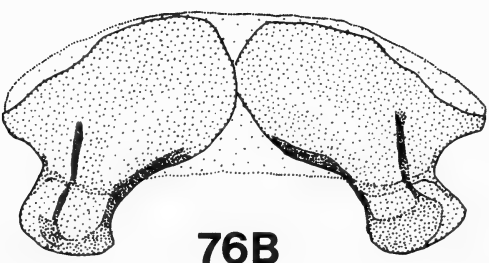
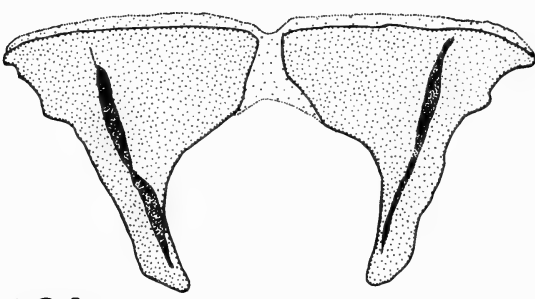
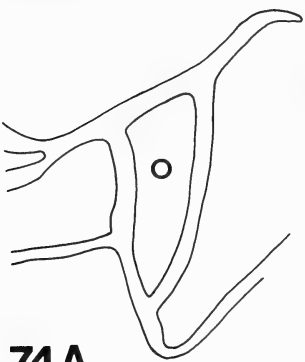
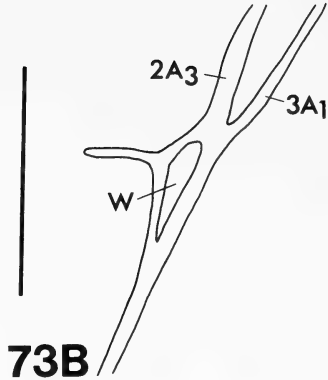
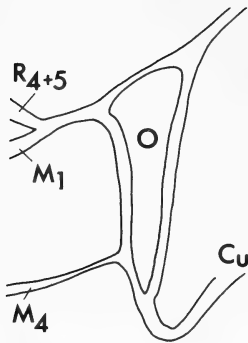
**Phylogenetic relationships.**— We believe that *Pinacodera* is the sister group of the ancestor of *Afrotarus* + *Cymindis* (sensu stricto), based on the inference that males of the common ancestor of subgenera *Pinacodera* + *Afrotarus* + *Cymindis* exhibited the autapotypic feature of the complex apical sclerite in the internal sac, as preserved in the descendant stocks. This requires loss of this sclerite from at least one descendant lineage of *Pinacodera*.

**A second hypothesis, based on the pattern of geographical distribution of *Cymindis* sensu lato** (*Pinacodera* confined to the New World, two of the other three subgenera confined to the Old World, and one with most of its species there), is that *Pinacodera* is the sister group of the ancestral stock of the other three subgenera. Such an hypothesis requires either independent gains of the genital sclerite (once in *Pinacodera* and once in the *Afrotarus* + *Cymindis* stock), or at least two losses of this sclerite (once from *Taridius*, and once from *Pinacodera*). Neither hypothesis is very well supported, but we think the first is rather stronger, requiring one less





Figs. 66–72. Line drawings of structure of Cymindina.—Pronota and genitalia. Figs. 66–68. Pronota, setae omitted, of *Cymindis (Afrotarus) nigra* (Andrewes). Figs. 69–72. Male genitalia of *Cymindis*. Fig. 69: *C. (Taridius) opacula* (Chaudoir), A and B, median lobe, left lateral and ventral aspects (various portions), respectively. Fig. 70: *C. (Afrotarus) kilimana* Kolbe, A and B, median lobe, left lateral and ventral aspects, respectively; C and D, left and right parameres, ventral aspect, respectively. Fig. 71: *C. (A). nigra* (Andrewes), A and B, median lobe, left lateral and ventral aspects, respectively. Figs. 72A–C: *Cymindis (sensu stricto) suturalis* Dejean, A and B, median lobe, left lateral and ventral aspects, respectively; C. internal sac, inverted position. Figs. 72D–E: *C. (sensu stricto) hieronticus* (Reiche), median lobe, left lateral and ventral aspects, respectively.



Figs. 73–76. Line drawings of structures of Cymindina.—Figs. 73–74. Wing veins and cells of *Cymindis* species, A and B, oblongum and wedge cells, respectively: 73, *C. (Taridius) opacula* (Chaudoir); 74, *C. (sensu stricto) suturalis* Dejean. Fig. 75. Color pattern of left elytron of *Cymindis (Taridius) stevensi* (Andrewes): A, *C. s. andrewesi* (van Emden); B, *C. s. nilgirica* (Andrewes). Fig. 76. Terminal abdominal sclerites of *C. (Pinacodera)* new species no. 1: A, Tergum VIII, dorsal aspect; B, Sternum VIII, ventral aspect; Tergum X, dorsal aspect. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M, media; R, radius.

loss of a complex structure, and not requiring its independent development in two lineages.

### Subgenus *Afrotarus* Jeannel, new status

Figs. 53, 59, 66-68, and 70-71

**Diagnostic description.**— Size small SBL ca. 5.0-7.0 mm. Color: body rufo-piceous to almost black, appendages somewhat paler. Microsculpture: head— vertex with meshes isodiametric, frons with meshes transverse or absent; pronotum with meshes transverse; elytra with meshes transverse or isodiametric; ventral surface with meshes generally transverse. Luster: head shining; pronotum and elytra shining to slightly iridescent; ventral surface generally slightly iridescent. Vestiture: dorsal surface of body glabrous (adults of most species) or sparsely setose (adults of one species), and dorsal surfaces of tarsomeres glabrous or setose. Head: frons each side with two or three sharply defined ridges extended longitudinally. Antennae various: antennomeres 4-10 each either average in proportions (l/w ca. 2.00) or shortened (l/w ca. 1.50). Pronotum (Figs. 66-68) transverse or only slightly wider than long, sides sinuate, lateral margins slightly elevated posteriorly. Metathorax reduced, metepisternum with lateral and basal margins subequal in length, or lateral margin distinctly longer than basal margin. Wings reduced to short stubs. Median lobe of male genitalia with apex hooked or straight; internal sac with sclerotized plate, as in subgenus *Cymindis* (Figs. 70A, 71A). Stylomere 2 of ovipositor with dorsal ensiform setae longer (Figs. 59A, B) or average.

**Included species.**— This subgenus includes five species: four African; one Arabian; and one Indian. The African species are: *C. kilimana* Kolbe; *C. leleupi* (Basilewsky); *C. meruana* (Basilewsky); and *C. raffrayi* Fairmaire. The Arabian species is *C. scotti* Basilewsky, and the Indian species is *C. nigra* (Andrewes).

**Notes about habitat.**— The species are known from mountain forests and their environs.

**Geographical distribution.**— The range of this subgenus includes the high mountains of east Africa (Kilimanjaro and Meru, in Tanzania), Ethiopia, the southern mountains in the Arabian Peninsula, and the hills in southern India. Two species (*C. kilimana* and *C. leleupi*) are known from a single massif (Kilimanjaro). The remaining species are allopatric relative to one another. However, all of these taxa are known from very few specimens.

**Phylogenetic considerations.**— Basilewsky (1962: 205-207) suggested that the extant species of *Afrotarus* (known to him only from Africa and Arabia) represented a Palaearctic lineage derived from *Cymindis* stock. Presence of the group in southern India suggests that it probably occupied lands farther north, an inference that could also be derived from Basilewsky's hypothesis. However, the evidence at hand does not require that *Afrotarus* be a southern derivative of a northern group. We think it likely that *Afrotarus* is relict, and is the sister group of subgenus *Cymindis*.

### Key to Species of Subgenus *Afrotarus* Jeannel

- 1 (0) Dorsal surface and eyes sparsely setose; median lobe of male genitalia with apical hook (Fig. 71). . . . . *C. (Afrotarus) nigra* (Andrewes), p. 155
- 1' Dorsal surface and eyes glabrous; apex of median lobe hooked or not . . . . . 2.
- 2 (1') Pronotum about as long as wide, impunctate, marginal grooves each broad throughout length, lateral margins elevated. Elytra subovoid, disc markedly flattened, marginal grooves deep, lateral margins elevated, microlines of intervals distinct. Head elongate, smooth, eyes small, hardly prominent, temples long. Antenna long, slender, three articles extended past base of pronotum. Labial tooth broad, rounded apically. Head and pronotum rufo-testaceous, elytra castaneous medially, testaceous marginally, and with large humeral mark testaceous. Length 8.00 mm. or more. . . . .

TABLE 4

DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (SBL) AND IN VALUES FOR THE RATIO  $Pl/PwB$  AMONG SPECIMENS OF *CYMINDIS NIGRA* (ANDREWES)

LOCALITY AND SEX	SBL (mm.)	$Pl/PwB$
Palni Hills ♀	5.46	0.94
Cardomon Hills ♂	5.02	1.03
Maharashtra ♂	6.54	1.02

- ..... *C. (Afrotarus) scotti* Basilewsky.
- 2' Pronotum transverse, wider than long, disc punctate or not, lateral margins not elevated. Head broad, eyes large and prominent, temples shorter. Antennomeres 4-10 short and wide, extended past base of pronotum only slightly more than two articles. Mentum with apex of tooth acute. Elytron with lateral margin plane, not elevated. Length 7.00 mm. or less ..... 3.
- 3 (2') Elytral intervals with microlines indistinct, meshes transverse, surface slightly iridescent. Pronotum 1.40 times wider than long, sides markedly constricted posteriorly, but not sinuate; posterior angles slightly projected. Elytra castaneous, with vague testaceous humeral markings in basal 0.25 of intervals 5 and 6 ..... *C. (Afrotarus) raffrayi* Fairmaire.
- 3' Elytral intervals with microlines less well developed, meshes isodiametric, dull 4.
- 4 (3') Elytra generally castaneous, each with testaceous mark on interval 3 anterior to middle, and another short one preapically . *C. (Afrotarus) leleupi* (Basilewsky).
- 4' Elytron with interneurs shallow, impunctate, uniformly piceous or bicolored with well developed humeral marks. Median lobe without apical hook ..... *C. (Afrotarus) kilimana* Kolbe.

*Cymindis (Afrotarus) nigra* (Andrewes), NEW COMBINATION

Figs. 66-68, and 71

We record a few observations about the limited material that we have seen of this species: three specimens from the proximally located Palni (type locality) and Cardomon Hills, and one specimen from Maharashtra, some 500 km. to the north. The male from Maharashtra differs rather strikingly from the more southern specimens: dorsal integument and eyes of the former are more evidently setose, lateral margins of the pronotum (Fig. 68 cf. Figs. 66 and 67) are more reflexed, elytral humeri are less constricted, the metepisternum is distinctly longer than wide, and body size is larger (Table 4). These differences suggest specific distinctness. On the other hand, the adult of *C. nigra* from the Cardomon Hills differs from specimens in the Palni Hills in form and proportions of pronotum (pronotum longer than wide, Table 4), and in color, though the localities are close together. This suggests that *C. nigra* is inherently variable, so

that one could imagine that populations that are far apart geographically could differ strikingly. Further, the apex of the median lobe of the northern male is identical in form to that of a male paratype. For now, we prefer to include all of these specimens in a single species, with the expectation that additional material will eventually be accumulated and will serve as the basis for a revision of this interesting complex.

One might expect that the Indian species of *Afrotarus* would exhibit a combination of features that would set it apart from the more western species which are geographically close to one another. In fact, this expectation is not realized, and the Indian species seems to differ no more from the African species than the latter differ from one another.

*Material examined.*— We have studied specimens of subgenus *Afrotarus*, labelled as follows.

*C. kilimana* Kolbe. Male and female, TANZANIA, Kilimanj. Sjostedt; Kiboscho 3000 m Mus Paris coll. Ch. Alluaud (MNHP).

*C. nigra* (Andrewes). Male, INDIA Madero Ind. Or.; Staudinger and Bang-Haas, 1933; H. E. Andrewes Coll. BM 1945-97 (BMNH). Female, Shores of Kodaikanal Lake, 6550 ft Palni Hills S. India VII.22 (under stones), S. Kemp (ZSIC). Female, S. INDIA 8 mi. NE Munnar, 6200' III.20.62; E. S. Ross, D. Q. Cavagnaro (CAS). Note: this locality is in the Cardomon Hills of the Western Ghats, and is also known as Pallivasal. Male, INDIA, Maharashtra Mahabaleshwar 1250 m. II.13.62; E. S. Ross, D. Q. Cavagnaro (CAS).

*C. raffrayi* Fairmaire. Male, ETHIOPIA Simien Derasghie c. 9800 ft. 22.XII.1952; from grove of tall juniper trees north of town; N. Ethiopia 1952-1953, Hugh Scott, 3 m, 1953-335; *Afrotarus raffrayi* Fairmaire, det. Basilevsky 1953 (BMNH).

### Subgenus *Cymindis* Latreille, NEW STATUS

Figs. 41A-D, 61A-B, 62A-B, 72A-B, 74A-B

Major recent faunal treatments of *Cymindis* are for: France, by Jeannel (1942a); Morocco, by Antoine (1962); eastern Asia, by Jedlička (1963); Japan, by Habu (1967); and the Nearctic Region, by Lindroth (1969a). V. M. Emetz is actively studying the eastern Palaearctic species. Perhaps in the near future, he will be able to write a general revision of the subgenus on a world-wide basis, and thus establish a general system.

*Diagnostic description.*— The faunal treatments listed above offer detailed characterizations of adults. Especially useful are the descriptions by Antoine and Lindroth. Here, we record only those features that serve to differentiate *Cymindis* adults from those of other subgenera, and that offer promise for establishing phylogenetic relationships.

Size average for carabids (length 7.0 - 12.0 mm.). Color various, dorsum varied from nearly black to rufous, or bicolored, with head and prothorax rufous, elytra darker (black or metallic blue); venter generally paler than dorsum; legs and mouthparts piceous to testaceous, generally paler than dorsum; elytra concolorous, or dark with pale humeral marks. Microsculpture developed or not, but if developed: meshes isodiametric on head and elytra, slightly transverse on pronotum. Luster: dorsal surface generally dull, pronotum more shiny than head or elytra, metallic in members of few species (group designated *Menas* Motschulsky). Vestiture: surface generally setose, though markedly reduced in members of some species (for example, *C. suturalis* Dejean, and *C. hieronticus* Reiche) to very sparse and very short setae, visible only in lateral aspect at high magnification; tarsomeres dorsally and antennomeres 1-3 setose. Surface generally punctate, though punctures reduced in specimens with reduced setation. Fixed setae average, though members of some species with additional lateral setae on pronotum; elytron with three or four setigerous punctures in interval 3. Head: frons each side with or without longitudinally extended ridges and grooves, frontal impressions indistinct. Antennae average for carabids, antennomere 3 distinctly longer than 4; antennomeres 4-10 each longer than wide. Mouthparts: mandibles as in Figs. 41A-D, right mandible with well developed anterior terebral tooth (Fig. 41A); terminal palpomeres similar in form, or labial of males of some species broader than maxillary; labial palpomeres of females unmodified. Pronotum slightly or markedly transverse, sides slightly sinuate or incurved evenly posteriorly; disc slightly convex; posterior angles rectangular or more or less rounded; base arcuate; metepisternum with lateral margin longer than anterior margin (*i.e.*, longer than wide). Elytra average for lebiines. Macropterous or brachypterous. Tarsal claws with denticles well developed, three or more (adults of most species), or very small, one or two. Median lobe of male genitalia with apical portion short, either straight or curved, apical orifice on left side (Figs. 72A-E); internal sac with fields of microtrichia, with apical sclerite (Fig. 72C). Stylocere 2 of ovipositor average for *Cymindis* (Figs. 62A-B).

*Included species.*— This subgenus is moderately diverse, including more than 150 species, but it is not very divergent (Antoine, 1962: 566). Thus it seems to be, in terms of its state of evolution, in full flower.

As Chaudoir (1873: 53) noted, *Cymindis* became a dumping ground (“une espèce de magasin”), including a collection of unrelated lebiines that shared in common terminal securiform palpomeres. He traced development of the concept of the genus that he had, which is essentially the one we use for the nominotypical subgenus. Csiki (1932: 1464) listed *Iscariotes* Reiche and *Psammoxenus* Chaudoir as subgenera of *Cymindis* (Chaudoir treated these groups as genera close to *Cymindis*). The subgenus *Tarulus* Bedel, 1906 was accepted as such by Csiki (1932: 1464). Jeannel (1942a) excluded *C. canigoulensis* (placed in the subgenus *Pseudomasoreus* by Desbrochers des Loges (1904), and similarly ranked by Csiki (1932: 1464)). Additionally, subgenera have been added to those listed by Csiki (1932: 1464-1465): *Pseudocymindis* Habu, 1967; *Paracymindis* Jedlička, 1968; *Assadera* Mandl, 1973; *Pteroritzella* Mandl, 1973; *Neopsammoxenus* Emetz, 1973; and *Pseudomastes* Emetz, 1972. We believe that all of these groups should be subordinate to the rank of subgenus, but that remains to be determined.

*Notes about habitat.*— According to Lindroth (1969a: 1071), and from our experience with the Nearctic fauna, the species are xerophilous, individuals living in open country with sparse vegetation. In forested regions, adults are found in open meadows, or along edges of forests. Populations of some species (for example, *C. arizonensis* Horn) inhabit deserts, while those of other species (for example, *C. borealis* LeConte) occur on dry arctic tundra.

*Geographical distribution.*— This subgenus is widespread in the Holarctic Region. In the Old World, it ranges from the Atlas Mountains in the west and Himalaya in the east northward to the Arctic. The range in the New World is similar: from northern Chihuahua, Mexico, to the Arctic Islands of Canada. Most species, however, are concentrated in the middle latitudes of the Northern Hemisphere.

*Phylogeny and zoogeography.*— We have three points to make. Judging from the numerous species identified by means of few characters, and wide continuous range of the subgenus, we believe its differentiation to be relatively recent. Because the group is much more diverse and divergent in the Old World than the New (all Nearctic species probably belong to a single Holarctic species group), and because its seemingly closest relatives are also in the Old World, we believe that *Cymindis* (*sensu stricto*) is of Old World origin. We also believe that the xerophily of the species is a derived feature that enabled the group to spread and diversify with the later Tertiary development of dry temperate habitats.

*Material examined.*— We have seen specimens of most Nearctic species, but we have studied and dissected only the following Old World forms.

*Cymindis suturalis* Dejean. Male and female, labelled: ALGERIA Biskra, Van Dyke Coll. (CAS).

*Cymindis hieronticus* Reiche. Four males labelled: W. PAKISTAN 10 mi. SW Kohat 650 m. XII.19.1961; E. S. Ross and D. Q. Cavagnaro. Four females, labelled: W. PAKISTAN, 2 mi. w. Cherat, 1200 m., XII.20.1961; E. S. Ross and D. Q. Cavagnaro.

### *Hystrichopus* Boheman

Figs. 44A-D, 52, 54, 58, 64, 77-88C

*Hystrichopus* Boheman, 1848: 42. GENERITYPE: *Hystrichopus angusticollis* Boheman, 1848 (subsequent designation by Basilewsky, 1954b: 15).— Péringuey, 1896: 212-218.— Basilewsky, 1954b: 7-80.— 1958: 297-302.— 1960: 85-86.— 1961b: 122-126.— 1962: 207-212.— 1976: 717.

*Plagiopyga* Boheman, 1848: 75. GENERITYPE: *Plagiopyga ferruginea* Boheman, 1848: 76 (monotypy). NEW SYNONYMY.— Péringuey, 1896: 212-221.— Basilewsky, 1945b: 80-94.— 1958: 302.

*Pseudomasoreus* Desbrochers des Loges, 1904: 140, 143, 163. GENERITYPE: *Cymindis canigoulensis* Fairmaire and Laboulbène, 1854: 32 (monotypy).— Bedel, 1906: 241.— Porta, 1923: 227.— Antoine, 1938: 171.— Jeannel, 1941: 62.— 1942a: 1039-1041.— 1949: 878-881.— Basilewsky, 1953b: 57-58.— 1954c: 89-96.— 1958a: 296-297.— 1962: 212-216.— Antoine, 1962: 562.— Mateu, 1970a: 173-175.— Basilewsky, 1976: 717.— Mateu, 1980: 16-23.

*Assadecma* Basilewsky, 1982: 20. GENERITYPE: *Assadecma madagascariensis* Basilewsky, 1982: 22 (original designation and monotypy). NEW SYNONYMY.

Data about synonymy are provided in conjunction with treatments of subgenera.

The following features of adults characterize this genus: head with two pairs of supraorbital setigerous punctures; frons without ridges and grooves laterally; elytron with lateral umbilicate punctures larger and thus clearly distinguishable from other setigerous punctures; right mandible with well developed premolar (Figs. 44B and D); median lobe of male catopic, internal sac without sclerites (Figs. 86C-88C); valvifer of ovipositor with extra lobe, stylomere 2 elongate, slender, with single ensiform seta (Figs. 55-57).

Jeannel (1942a) established the tribe Pseudomasoreini for *Pseudomasoreus* Desbrochers des Loges, adding to it (1949) *Hystrichopus* Boheman. Subsequently, Basilewsky (1954b), who treated this group as a tribe of Lebiinae equivalent to the Cymindini and other lebiine tribes, added *Plagiopyga* Boheman. Three years later, Basilewsky (1957: 240) noted that male dromiines of *Klepturus* and *Kleptromimus* also had catopic median lobes, and concluded that it would be necessary to re-evaluate this character state as a basis for ranking the pseudomasoreine group as a tribe of Lebiinae. With Mateu (1980: 17) we believe that this feature does not constitute a sufficient basis for giving pseudomasoreines a high rank, though in contrast to him, we believe that catopy was evolved only once in the Cymindina, and thus delimits a monophyletic group.

#### Subgenus *Pseudomasoreus* Desbrochers des Loges, 1904, NEW STATUS

*Characteristics.*— This subgenus is adequately characterized by Jeannel (1942a and 1949), Basilewsky (1954a), and Antoine (1962). To the features noted by these authors, we add: stylomere 2 of ovipositor slender throughout length, more or less tubular, with dorso-lateral ensiform setae moderate to long (Fig. 55A).

*Included species.*— This subgenus includes 13 previously described species, and four more from localities in the Union of South Africa, are described below.

*Geographical distribution.*— The range of *Pseudomasoreus* extends from the Cape Region of the Union of South Africa to the Pyrenees Mountains of Spain and France, and includes Madagascar. However, the range is discontinuous: five species are known only from South Africa (see below); nine species are known only from Madagascar (Mateu, 1980); two species are known only from the high mountains of East Africa (Basilewsky, 1962); and *P. canigoulensis* is known only from localities in and to the north of the Atlas Mountains.

*Notes about phylogeny and zoogeography.*— Mateu (1980: 15), in conjunction with his useful revision of the Madagascan species, notes that they seem to be montane- adapted and possibly xerophilous, but that little is known about their way of life. Most species (including those in Africa) are known from single localities, only. Mateu also noted the relative abundance of species of Madagascar compared with those on the African continent, and suggested that additional species may be discovered. He stated that the subgenus, though truly old, seems to have been revitalized on Madagascar, for its species there are very similar to one another, and thus seem to have evolved recently.

Jeannel (1942b: 316-317), when species were known only from Madagascar and north of the Atlas Mountains, suggested that *Pseudomasoreus* had arisen in eastern Africa during the



Cretaceous, had reached the two areas listed above, and survived there, but had become extinct on mainland Africa, to the south of the Sahara. Subsequent discovery of *H. capicola*, *H. kivuanus*, and *H. uluguruanus* confirmed Jeannel's prediction that the group had been in Afrotropical mainland Africa. Basilewsky (1954c: 91), when he described *H. capicola*, predicted that the group would also be represented on the mountains of East Africa. Thus, his more detailed prediction was confirmed with discovery of *H. kilimanus hkbj* and *H. uluguruanus*.

Both Jeannel and Basilewsky stated that *Pseudomasoreus* had arisen in Cretaceous time, and had once been continuously distributed. Thus, the present discontinuous range is interpreted as relict, and these authors suggested that *Pseudomasoreus* is on the way to extinction. This may be true, but it is interesting to note that the northern periphery of the range of the group is occupied by a species whose adults are macropterous. It thus seems possible that this lineage may be a recent arrival in the north. However, until phylogeny can be reconstructed and used as a basis for interpreting the distribution pattern, it seems best to avoid making additional inferences.

## The Species of *Pseudomasoreus* of East and South Africa

We have had the opportunity to study 16 specimens of *Pseudomasoreus* from Afrotropical localities. These represent material of three described species and four undescribed species. We describe the latter and provide a key to these and to the previously described mainland Afrotropical species.

*Description.*— We list here features shared by adults of all of the species.

Color. Generally somber, dorsal surface various, lateral margins of pronotum and elytra generally a bit paler than medial areas; ventral surface constantly dark (rufo-piceous to piceous); appendages flavous.

**Microsculpture.** Dorsum of head (including clypeus) and labrum with meshes isodiametric; pronotum with meshes various; meshes of pro- and pterothoracic sterna and metepisterna transverse; meshes of pro- and mesepisterna elongate; meshes of abdominal sterna transverse. Luster of dorsal surface various; of ventral surface, iridescent.

**Eyes.** Moderate in size, flattened, not prominent.

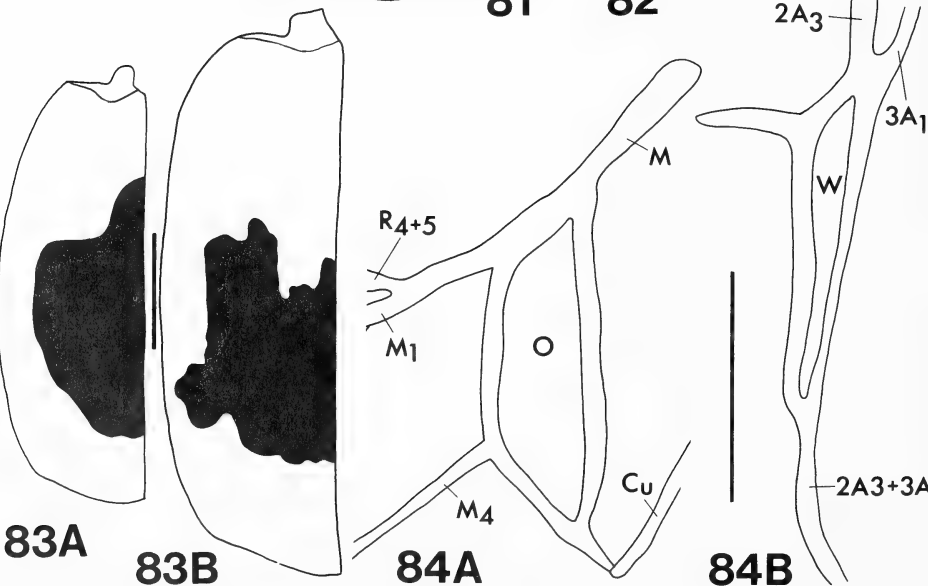
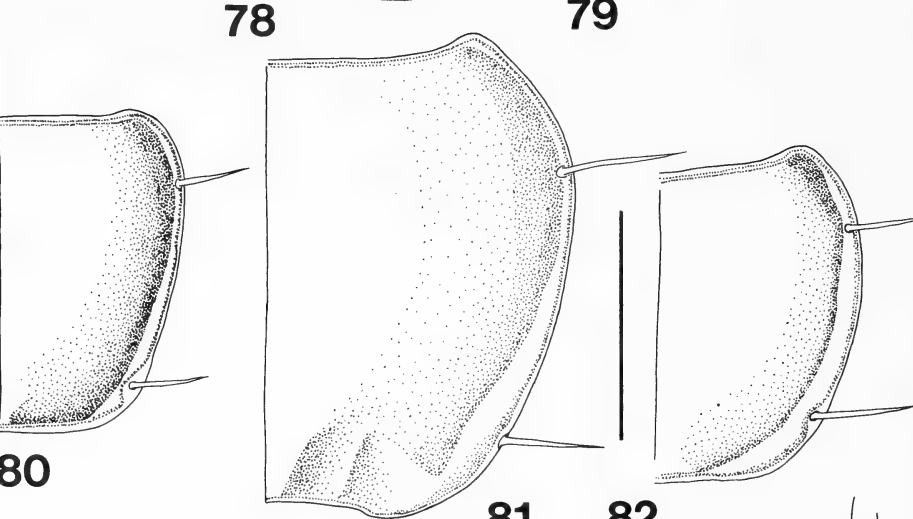
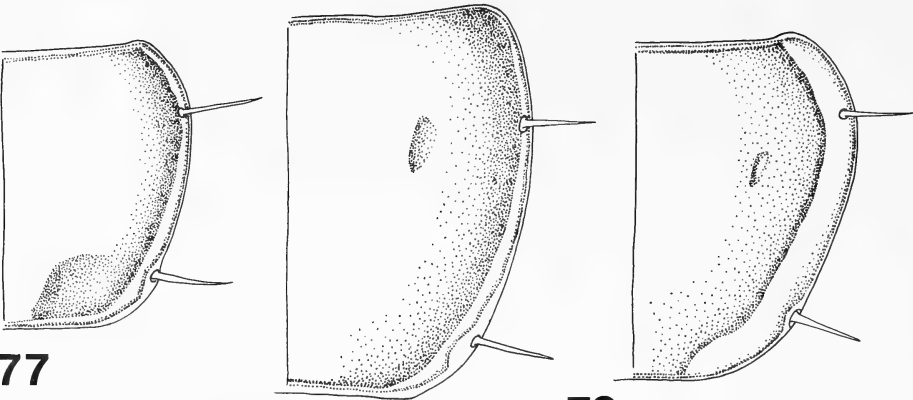
Pronotum (Figs. 77-82). Subcordate to cordate, sides incurved posteriorly; posterior angles obtuse; disc with median longitudinal impression and laterally with irregular shallow impressions, without transverse impressions; surface slightly convex, laterally slightly sloped; lateral grooves well developed, posterior lateral impressions irregular shallow basins, more or less continuous with lateral grooves. Two pairs of lateral setae.

Elytra flat; posterior margins subtruncate. Interneurs average, impunctate; scutellar interneur developed. Intervals slightly convex, sparsely punctate. Parascutellar setigerous puncture developed. Disc with two setigerous punctures in interval 3; umbilical series including about 14 setigerous punctures.

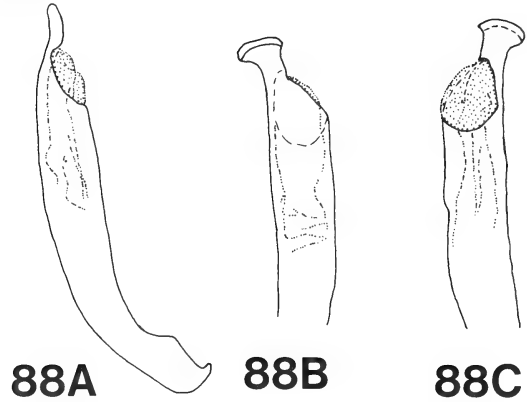
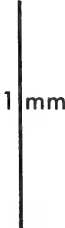
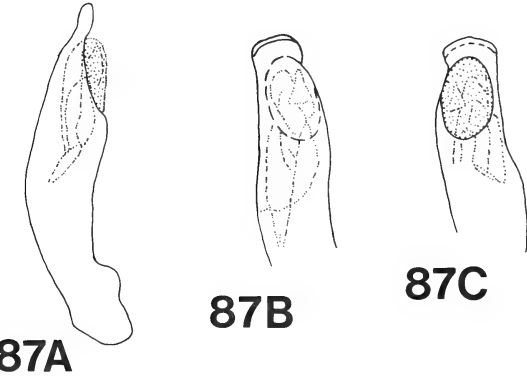
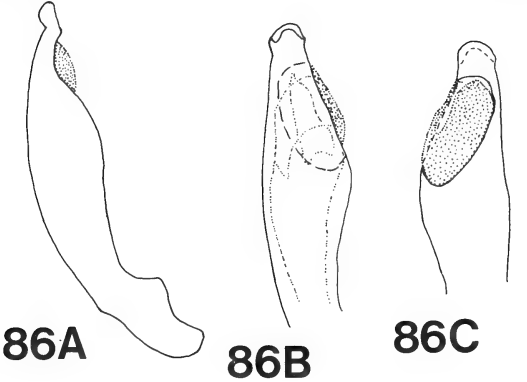
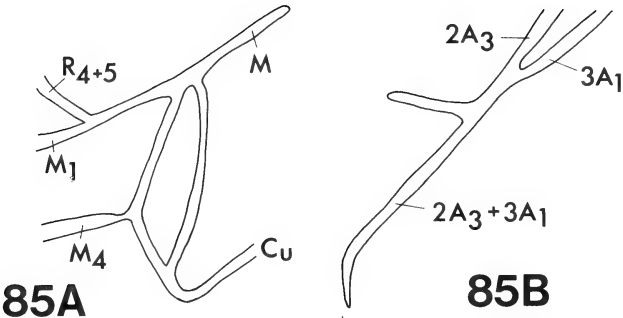
*Relationships.*— The data are not available to do more than arrange the species in order of increasing apotypy, based on inferred morphoclines of changes in microsculpture (from isodiametric to transverse meshes) and structural changes associated with loss of wings (reduction of metathorax, and change in form of elytral humeri). We also assume that these species are more closely related to one another than they are to the Madagascan species of *Pseudomasoreus* or to the Mediterranean *P. canigoulensis*.

### Key to Eastern and Southern African Species of the Subgenus *Pseudomasoreus* Desbrochers des Loges

- |    |     |  |    |
|----|-----|--|----|
| 1  | (0) | Elytron with microsculpture meshes isodiametric                          | 2  |
| 1' |     | Elytron with microsculpture meshes transverse, surface iridescent or not | 3. |
| 2  | (1) | Metepisternum elongate (w/l = ca. 1.50); size smaller (SBL ca. 5.00 mm)  |    |
|    |     | <i>H. (Pseudomasoreus) reticulatus</i> new species, p. 164               |    |
| 2' |     | Metepisternum short (w/l ca. 1.00); size larger (SBL more than 6.00 mm)  |    |



Figs. 77–84. Line drawings of structures of Cymindina.—Figs. 77–82. Pronota, dorsal aspect, of *Hystrichopus* (*Pseudomasoreus*) species: 77, *H. reticulatus*, new species; 78, *H. capicola* (Basilewsky); 79, *H. uluguruanus* (Basilewsky); 80, *H. basilewskyi*, new species; 81, *H. thoracicus*, new species; 82, *H. mateui*, new species. 83A, *H. kivuanus* (Basilewsky); 83B, *H. mateui*, new species. Fig. 84. Wing cells and associated veins of *Hystrichopus* (*sensu stricto*) *massaicus* Basilewsky: A, oblongum cell; B, wedge cell. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M, median; R, radius.



Figs 85–88. Line drawings of structures of Cymindina.—Fig. 85. Wing cells and associated veins of *Hystrichopus (Plagiopyga) chaudoiri* Péringuey: A, oblongum cell; B, wedge cell. Figs. 86–88. Male genitalia, median lobe of *Hystrichopus (Pseudomasoreus)* species. A, B, C, left lateral, dorsal, and ventral aspects (basal lobe excluded), respectively, of: 86, *H. uluguruanus* (Basilewsky); 87, *H. basilewskyi*, new species and 88, *H. mateui*, new species. Legend. Wing cells: O, oblongum; W, wedge. Veins: A, anals; Cu, cubitus; M, media; R, radius.

- ..... *H. (Pseudomasoreus) capicola* Basilewsky, p. 167
- 3 (1') Metepisternum long and slender (w/l more than 1.50); microsculpture meshes of elytron wide, surface not iridescent; elytron with dark mark behind middle (Fig. 83A) ..... *H. (Pseudomasoreus) kivuanus* Basilewsky, p. 167
- 3' Metepisternum short (w/l less than 1.50); elytra iridescent, bicolored or not . . . 4.
- 4 (3') Elytron with distinct dark mark near suture, rest of surface rufo-flavous . . . . . 5.
- 4' Elytron concolorous, rufo-piceous to piceous . . . . . 6.
- 5 (4) Specimen from locality in South Africa; pronotum less markedly constricted posteriorly; dark mark of elytron extended more anterad (Fig. 83B); male with apical portion of median lobe long, inclined to left (Figs. 88B, C) . . . . .
- ..... *H. (Pseudomasoreus) mateui*, new species, p. 170
- 5' Specimen from Tanzania; pronotum markedly narrowed posteriorly; dark mark of elytron not extended anterad; male with apical portion of median lobe straight . . . . . *H. (Pseudomasoreus) uluguruanus* Basilewsky, p. 168
- 6 (4') Metepisternum slightly longer than wide (w/l 1.25- 1.38); smaller (SBL ca. 5.00 mm.) . . . . . *H. (Pseudomasoreus) basilewskyi* new species, p. 168
- 6' Metepisternum about quadrate, length less than width; larger (SBL ca. 7.00 mm) . . . . . *H. (Pseudomasoreus) thoracicus*, new species, p. 169

*Hystrichopus (Pseudomasoreus) reticulatus*, new species

Fig. 77

HOLOTYPE female, labelled: COLL MUS TERVUREN Cape Prn: Clanwilliam distr., Sederberg VII.1958 1500m J. Smith (MACT).

*ion of specific epithet.*— A Latin adjective, meaning net-like, in allusion to appearance of the isodiametric microsculpture of the elytra.

*Recognition.*— In addition to features cited in the key, the single female of this species differs from females of *H. capicola* having a wider pronotum in relation to length (see Table 7). From females of other species, this one differs in having the pronotum narrow in relation to head width (see Table 6).

*Description.*— Values for SBL and for ratios Hw/Pmw, Pl/Pmw and MES: l/w are presented in Tables 5-8.

Color. Dorsum piceous; epipleura of elytra rufous.

Microsculpture. Dorsum of head and elytra with isodiametric meshes, pronotum with wide, transverse meshes.

Luster. Surface generally dull.

Pronotum. As in Fig. 77. Sides not markedly constricted posteriorly.

Elytra. Humerus rounded, not projected anteriorly. Basal ridge not markedly sinuate.

Ovipositor. Stylocere 2 longer and straighter, and with ensiform setae shorter than in *H. mateui*.

*Geographical distribution.*— This species is known only from the type locality in the Union of South Africa.

*Relationships.*— The long metepisternum, rounded elytral humeri, and isodiametric microsculpture of the elytra indicate that this is the most primitive species of *Pseudomasoreus* on mainland Africa.

*Material examined.*— Known only from the holotype.

TABLE 5  
DATA ABOUT VARIATION IN STANDARDIZED BODY LENGTH (MM) AMONG  
EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

SPECIES	MALES		FEMALES	
	N	RANGE	N	RANGE
<i>H. reticulatis</i>			1	4.92
<i>H. capicola</i>			3	6.12–6.24
<i>H. kivuanus</i>			1	6.28
<i>H. uluguruanus</i>	2	5.20–5.56	1	5.32
<i>H. basilewskyi</i>	2	5.00–5.36	2	5.04–5.20
<i>H. thoracicus</i>			3	6.84–7.12
<i>H. mateui</i>	1	5.00	2	5.40–5.68

TABLE 6  
DATA ABOUT VARIATION IN VALUES FOR THE RATIO Hw/Pmw  
AMONG EAST AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

SPECIES	MALES		FEMALES	
	N	RANGE	N	RANGE
<i>H. reticulatus</i>			1	0.78
<i>H. capicola</i>			3	0.78–0.80
<i>H. kivuanus</i>			1	0.69
<i>H. uluguruanus</i>	2	0.73	1	0.76
<i>H. basilewskyi</i>	2	0.75–0.77	2	0.78
<i>H. thoracicus</i>			3	0.68–0.72
<i>H. mateui</i>	1	0.77	2	0.72

TABLE 7  
DATA ABOUT VARIATION IN VALUES FOR THE RATIO  $Pl/P_{mw}$  AMONG EAST  
AND SOUTH AFRICAN SPECIES OF *PSEUDOMASOREUS*

SPECIES	MALES		FEMALES	
	N	RANGE	N	RANGE
<i>H. reticulatis</i>			1	0.78
<i>H. capicola</i>			3	0.82–0.85
<i>H. kivuanus</i>			1	0.69
<i>H. uluguruanus</i>	2	0.75	1	0.75
<i>H. basilewskyi</i>	2	0.85–0.86	2	0.83–0.84
<i>H. thoracicus</i>			3	0.76–0.78
<i>H. mateui</i>	1	0.77	2	0.72

TABLE 8  
DATA ABOUT VARIATION IN VALUES FOR THE RATIO  $MES: 1/w$   
AMONG EAST AND SOUTH AFRICAN SPECIES OF  
*PSEUDOMASOREUS*

SPECIES	MALES		FEMALES	
	N	RANGE	N	RANGE
<i>H. reticulatus</i>			1	1.52
<i>H. capicola</i>			1	1.00
<i>H. kivuanus</i>			1	1.80
<i>H. uluguruanus</i>	2	1.00	1	1.00
<i>H. basilewskyi</i>	2	1.25–1.38	2	1.28–1.32
<i>H. thoracicus</i>			3	0.86–0.97
<i>H. mateui</i>	1	0.76	2	0.72–0.96



*Hystrichopus (Pseudomasoreus) capicola* (Basilewsky), NEW COMBINATION  
Figs. 55A-B, and 78.

*Pseudomasoreus capicola* Basilewsky 1954c: 93. HOLOTYPE female, labelled: HOLOTYPE [orange paper]; COL. MUS. CONGO. Cape Colony Dunbrody Co. P. Basilewsky; *Pseudomasoreus capicola* n. sp. P. Basilewsky det. 1954. (MACT). TYPE LOCALITY.—Dunbrody Cape Colony, South Africa.—Basilewsky, 1958a: 296-297, Fig. 40.

**Recognition.**—Large size, slender pronotum in relation to length and width of head, short metepisterna, isodiametric microsculpture of elytra, and slightly transverse microsculpture meshes of pronotum distinguish this species from others of *Pseudomasoreus*.

**Description.**—Tables 5-8 provide data about variation in SBL, and in values for ratios Hw/Pmw; Pl/Pmw and MES: l/w.

Color. Dorsum piceous, epipleura of elytra rufous.

Microsculpture. Head and elytra with meshes isodiametric, pronotum with meshes slightly transverse.

Luster. Dull.

Pronotum (Fig. 78) Narrow, sides slightly constricted posteriorly.

Elytra. Humeri projected forward, basal ridge markedly sinuate.

**Geographical distribution.**—This species is known only from the Union of South Africa, in Cape Province and Basutoland.

**Relationships.**—These have not been determined. The predominantly isodiametric microsculpture of the dorsum suggests that this species is primitive. However, the metathorax is appreciably shortened, suggesting some derivativeness.

**Material examined.**—In addition to the holotype, we have seen two females labelled: S. Afr. Basutoland Makhere Mts. 15 miles ENE Mokhotlong 8.IV.51 No. 268 Swedish South Africa expedition 1950-51 Brinck Rudebeck 9500 ft; COLL MUS CONGO (ex Lund Mus) Coll. P. Basilewsky (MACT). Six more specimens are known from this locality (Basilewsky, 1958a: 297), but we have not seen them.

*Hystrichopus (Pseudomasoreus) kivuanus* (Basilewsky), NEW COMBINATION  
Fig. 83A

*Pseudomasoreus kivuanus* Basilewsky, 1962: 215. HOLOTYPE, female, labelled: HOLOTYPE [orange paper]; COLL MUS CONGO Tanganyika Terr: Kilimanjaro Marangu Versant S.E. 1800-2200 m 20/27.VII.57; Resideu de foret transition [blue paper]; Mission Zoologiq. IRSAC en Afrique orientale P. Basilewsky et N. Leleup; *Pseudomasoreus kivuanus* n.sp. P. Basilewsky det. 1960 (MACT).

**Recognition.**—In addition to character states listed in the key, the female of *H. kivuanus* is distinguished by moderate size (SBL- 6.28 mm.) (smaller than the type of *H. thoracicus*, about same as females of *H. capicola*), and the pronotum very broad in relation to both head width (Table 6) and pronotum length (Table 7).

**Description.**—Data about Standardized Body Length, and ratios Hw/Pmw, Pl/Pmw, and MES: w/l are presented in Tables 5 to 8.

Color. Head and pronotum piceous, elytra generally rufous with broad, irregular, transverse dark mark in posterior half (Fig. 83A); elytral epipleura rufous.

Microsculpture. Meshes of head and pronotum isodiametric; meshes of elytra transverse.

Luster. Head and pronotum dull. Elytra shining, but not iridescent.

Pronotum. Very broad, sides rounded, moderately constricted posteriorly.

Elytra. Humeri average, not extended anteriorly as prominent lobes; basal ridge not markedly sinuate. Hind wing with cells as in Figs. 84A, B.

Basilewsky (1962: 215) stated that adults of this species were apterous. However, wing rudiments are about half the length of the elytra.

**Geographical distribution and habitat.**—The single known female was collected in Tanzania, on Mount Kilimanjaro, in forest, between 1800 and 2200 meters above sea level.

**Relationships.**—Color pattern and geographical proximity suggest that *H. kivuanus* and *H. uluguruanus* are more closely related to one another than to other species of

*Pseudomasoreus*. Their immediate common ancestor was probably from a primitive stock, for *H. kivuanus* has very slightly derived microsculpture of the dorsal surface, has retained long wing rudiments and features associated with wing reduction are not well developed; that is, the metathorax is large (as shown by long metepisterna), and the elytral humeri are not projected forward.

*Hystrichopus (Pseudomasoreus) uluguruanus* Basilewsky, NEW COMBINATION

Figs. 79 and 86

*Pseudomasoreus uluguruanus* Basilewsky, 1962: 213. HOLOTYPE male, labelled: HOLOTYPE [orange paper] ; vert foret/ombrophile dans l'humus [blue paper] ; COLL MUS CONGO Tanganyika Terr: Bunduki, Uluguru Mts., 1300 m. 2.5.1957; Mission Zoologique IRSAC en Afrique Orientale (P. Basilewsky and N. Leleup); *Pseudomasoreus uluguruanus* n. sp. P. Basilewsky det. 1960. (MACT). PARATYPE male, similarly labelled to holotype, but collected on summit of Mt. Kidunda, 1800-1950 m., 3.V.1957. (MACT). PARATYPE female, similarly labelled to holotype, but collected on Mgeta, 1300 m., 30.IV- 2.V. 1957. (MACT).

**Recognition.**— In addition to character states listed in the key, members of this species are recognized by a combination of small size (SBL less than 6.00 mm.), and cordate pronotum (Fig. 79).

**Description.**— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

**Color.** Head piceous; pronotum with disc piceous, broad lateral area rufous; elytra generally rufo-flavous, with broad irregular transverse dark mark in posterior half, less distinct in similarly marked female of *H. kivuanus*. Elytral epipleura flavous.

**Microsculpture.** Head with meshes isodiametric; pronotum with meshes isodiametric to transverse; elytra, with meshes transverse, narrow.

**Pronotum.** Form as in Fig. 79, cordate, sides constricted posteriorly.

**Elytra.** Humeri produced anteriorly as lobes, basal ridge of elytron markedly sinuate.

**Male genitalia.**— Median lobe as in Figs. 86A-C: apical portion in dorsal aspect short and broad; internal sac with basal microtrichial fields short, concentrated near apical orifice of median lobe (two males dissected).

Basilewsky (1962: 213) stated that specimens of this species are winged. However, each wing comprises a small stub only, no longer than the combined lengths of two abdominal terga.

**Geographical distribution and habitat.**— This species is known only from the type locality—The Uluguru Mountains in Tanzania, at elevation of 1800-1900 m. Adults were collected in mountain forest, in leaf litter.

**Relationships.**— Color pattern and geographical distribution indicate that *H. uluguruanus* and *H. kivuanus* are sister species. However, *H. uluguruanus* shares with the more derived species of *Pseudomasoreus* transverse microsculpture and iridescent luster of the elytra, reduction of wings, marked reduction of the metathorax (indicated by short metepisterna), and produced elytral humeri. Evidently, these states were developed convergently with the same states in other members of the subgenus.

*Hystrichopus (Pseudomasoreus) basilewskyi*, new species

Figs. 80 and 87

HOLOTYPE male, labelled: COLL MUS TERVUREN Cape prov. Swellendam distr., Grootvadersbos J. Smith VII.1958. (MACT). ALLOTYPE female, same label as holotype. Holotype and female paratypes returned to MACT; male paratype deposited in CAS.

**Derivation of specific epithet.**— We take pleasure in naming this species for Pierre Basilewsky, distinguished specialist of the African carabid fauna and of African biogeography.

**Recognition.**— In addition to key character states, small size, concolorous elytra, and metepisternum slightly longer than wide, distinguish members of this species from all others.

Males are further distinguished by the very short and broad apical portion of the median lobe (Fig. 87B, C).

**Description.**— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Head, rufo-testaceous; pronotum rufous; elytra rufo-piceous to piceous.

Microsculpture. Head with meshes isodiametric. Pronotum with meshes transverse, but not especially narrow; elytra with meshes transverse, very narrow.

Luster. Dorsum of head dull; pronotum with surface shining, not iridescent. Elytra with surface iridescent.

Pronotum. Form as in Fig. 80, moderately broad in relation to head, sides not markedly constricted posteriorly.

Elytra. Humeri projected anteriorly, basal ridge markedly sinuate.

Male genitalia. Median lobe (Fig. 87A-C) with apical portion very short and broad. Internal sac with basal microtrichial fields long, extended anteriorly in inverted position.

**Geographical distribution.**— This species is known only from the type locality, in South Africa.

**Relationships.**— This is a markedly derived species, adults having iridescent elytra and humeri projected. However, the metathorax is only partially reduced, and microsculpture of the pronotum is not modified enough to provide iridescence. Iridescence of the elytra is an apotypic character state shared with *P. thoracicus* and *P. mateui*, and on this basis we locate *P. basilewskyi* in an informal group with these species.

**Material examined.**— This species is known only from the type series.

#### *Hystrichopus (Pseudomasoreus) thoracicus*, new species

Fig. 81

HOLOTYPE female, labelled Grahamstown 14.1.1904 (J. O'N) [handwritten]; *Platynus* sp. nov. [handwritten]; *Pseudomasoreus* sp. ign. [handwritten] South African Museum. PARATYPES, two females, labelled: [G or A]? T, 15.V.12; S. Africa Cle Deux acc. 67769. (USNM). And as above, except "Cle Doux" (USNM).

**Derivation of specific epithet.**— This is an adjectival form of "thorax", and draws attention to the large pronotum that is characteristic of specimens included in this species.

**Recognition.**— Large size (SBL about 7.00 mm.), iridescent pronotum and elytra, and broad pronotum with wide lateral grooves distinguish adults of this species from other known Afrotropical species of *Pseudomasoreus*.

**Description.**— Data about variation in Standardized Body Length and in values for ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

Color. Dorsum of head, pronotum and elytra piceous, elytral epipleura rufous.

Microsculpture.— Head with meshes isodiametric; pronotum and elytra with meshes transverse, narrow.

Luster. Dorsum of head dull; pronotum and elytra with surfaces iridescent.

Pronotum. As in Fig. 81, cordate, lateral grooves wider than usual.

Elytra. Humeri projected anteriorly, basal ridge markedly sinuate.

Ovipositor. Stylomere 2 average for subgenus *Pseudomasoreus*.

**Geographical distribution.**— This species is known from the Union of South Africa, only.

**Relationships.**— This is a derived species in that its adults are characterized by iridescent pronotum and elytra, markedly reduced metathorax, and produced elytral humeri. These character states are shared with adults of *H. mateui*, new species, which we regard as the sister species of *H. thoracicus*.

*Hystrichopus (Pseudomasoreus) mateui*, new species

Figs. 82, 83B and 88A-C

**HOLOTYPE** male, labelled: Malvern, Natal; G. A. K. Marshall 1917-55 [blue line in middle of label]; Cymindide gen et sp nova? Per. [handwritten] (BMNH). **ALLOTYPE** female, labelled: NATAL Ekombe For. 39 mi. N. of Kranskop 1520 m. IV.10.58; E.S. Ross and R.E. Leech, collectors (CAS). **PARATYPE** female, labelled: Mbabang Swaziland [handwritten]; *Pseudomasoreus* n. sp. (ap. capicola Basilw) P. Basilewsky det. 1962 other specimens are necessary [Note: the left mandible missing]. (SAMC).

**Derivation of specific epithet.**— This is based on the surname of Dr. Joaquin Mateu, who has published extensively about carabids of the tropics of the world, especially about lebiines.

**Recognition.**— In addition to the key character states, specimens of this species are distinguished by small size (SBL less than 6.00 mm.) and cordate pronotum (Fig. 82). Males have a long apical portion of the median lobe, with apex spatulate (Figs. 88B, C).

**Description.**— Data about variation in Standardized Body Length, and in ratios Hw/Pmw, Pl/Pmw, and MES: l/w are presented in Tables 5 to 8.

**Color.** Head rufo-piceous; pronotum piceous to disc rufo-piceous, with lateral areas rufo-flavous (specimen may be slightly teneral); elytra with dorsal surface generally rufous to rufo-flavous, medially with dark mark extended along suture into basal half.

**Pronotum.** As in Fig. 82, cordate, sides markedly constricted posteriorly.

**Elytra.** Humeri projected anteriorly, basal ridge markedly sinuate. Hind wing with cells as in Fig. 84B.

**Male genitalia.** Median lobe (Figs. 88A-C) long, with apical portion long, spatulate. Internal sac with microtrichial fields long, extended basally.

**Ovipositor.** Stylomere 2 average for *Pseudomasoreus*.

**Geographical distribution.**— This species is known only from two localities in the Union of South Africa.

**Relationships.**— This species seems to be the sister species of *H. thoracicus*, new species.

Subgenus *Assadecma* Basilewsky, NEW STATUS

**Characteristics.**— The most striking features of this subgenus are: size of specimens (overall length 14 to 15 mm., estimated SBL 12 to 13 mm.), relative size of pronotum (almost half the length of elytra), its form (parallel-sided, base and apex about equal in width), very short and broad tarsomere 4, armature of the male internal sac (several rows of spines), and long, slender apical portion of the median lobe. Mandibles are markedly different from those of other cymindines, but we judge from the illustration (Basilewsky, 1982: Fig. 2c) of the ventral surface of the right mandible that it is worn. If so, the features exhibited are not of taxonomic value.

Other character states are shared with members of other subgenera of *Hystrichopus*. Even though females of *Assadecma* are not available, we believe that they will be found to have stylomeres characteristic of *Hystrichopus (sensu lato)*, and probably characteristic of subgenus *Pseudomasoreus*.

**Included species.**— The single known species of this subgenus, *H. madagascariensis* (Basilewsky), is based on two males, collect at different localities in eastern Madagascar. The type locality is Hiaraka (1000 meters), on the Masoala Peninsula. The holotype is in MNHP, the paratype in MACT.

**Notes about phylogeny.**— Relatively large size of its members, a markedly distinctive combination of other character states, and seeming isolation of the single known species on Madagascar suggest that *Assadecma* is a phylogenetic relic, rather than representing a recently

evolved descendant of one of the other extant subgenera. Thus, this taxon is likely to be of substantial importance in reconstructing the evolutionary history of *Hystrichopus* (*sensu lato*).

Subgenus *Hystrichopus* (*sensu stricto*) Boheman, new status

Figs. 44A-D, 52, 56A-B, 64, and 84A-B

*Notes about synonymy.*— Basilewsky (1954b: 13) listed the following genus-group names as junior synonyms: *Ctenoncus* Chaudoir, 1850; and *Assotatus*, *Assoterus*, *Astus*, and *Aspastus* Péringuey, 1896. He discussed the nomenclatural history of *Hystrichopus* and its junior synonyms (1954a: 15-16). Details are not reviewed here.

*Characteristics.*— This subgenus was adequately characterized by Basilewsky (1954b: 13-14), for purposes of identification. He did not, however, examine the mandibles (Figs. 44A-D), hind wings (oblongum cell large, Fig. 84A, wedge cell small, Fig. 84B) or stylomere 2 of the ovipositor (Fig. 56A): note the very short ensiform seta).

*Notes about classification.*— This subgenus includes 58 described, and two undescribed species. In spite of this diversity, *Hystrichopus* seems quite homogeneous, so much so that Basilewsky (1954b: 16) chose not to recognize formal subgenera, but instead arranged the species in two sections and 11 groups, to which he also assigned those species that he described subsequently.

Although many of the most closely related taxa are allopatric, Basilewsky elected not to use the subspecies category. He argued that more information was required to establish subspecies than species, and that he did not have the requisite information because of a shortage of specimens. He also argued that the brachypterous montane vicariads had been isolated long enough to have differentiated to the species level.

The two sections of *Hystrichopus* are distinguished by differences in development of the metathorax, which are in turn associated with wing development: adults of Section I have long metepisterna, dehiscent elytra, and are either macropterous or brachypterous; those of Section II have reduced metepisterna, elytra more or less fused together along the suture, and wings absent.

Although wing loss is characteristic of both groups, Basilewsky stated that processes of change were probably different: reduction of the flight function in Section II he recognized as an orthogenetic process, whereas wing loss by members of Section I was adaptive. The important point to note here is that he conceived the sections (as well as "Groups") as phylogenetically valid assemblages.

Nonetheless, in our view, wing loss in both sections is the result of the same process, that of adaptation. Furthermore, in the absence of additional evidence that Section II is monophyletic, this taxon must be suspect in a phylogenetic system: reduction of the metathorax could have taken place in a number of lineages independently. Section I is based on a symplesiotypy, and may not be monophyletic, either.

*Habitat.*— Basilewsky (1954b: 18) classified the species as "lapidicoles" or "humicoles". Lapidicoles are found under stones at lower elevations in savanna land, mainly in South Africa, but also at high altitudes in East Africa. Humicoles are residents of mountain forests, and are found in damp humus (leaf litter, *et al.* Adults do not show a tendency for reduction of pigment or eye size, so it seems certain that they are not associated with deep litter, nor are they troglaphiles.

Altitudinal range extends from near sea level in the south to between 3000 to 4000 meters on Mount Kilimanjaro, in Tanzania. Generally, the more northern taxa live at elevations above 1800 meters.

*Geographical distribution.*— The range of this subgenus extends from southernmost South Africa northward to the southeastern mountains of the Arabian Peninsula, and with an isolated species (*H. nimbanus* Basilewsky) on the massif of Nimba, in French Guinea, West Africa. The range is discontinuous, because the East African species occur on mountains, at high elevations.

The species of Section II seem to be restricted to South Africa and Zimbabwe. The range of the species of Section I is co-extensive with range of the subgenus as a whole.

*Notes about phylogeny and zoogeography.*— Basilewsky did not attempt to reconstruct the phylogeny of subgenus *Hystrichopus* in detail. However, he considered the topic in a general way (1954b: 21-23; see also 1962: 207-212). The distribution pattern (especially the marked isolation of *H. nimbanus* in the mountains of French Guinea), suggested to him that the group is ancient, at least earlier in origin than development of the Red Sea. The group was formerly widespread in Africa, and had wider ecological tolerances than have the extant stocks. Thus, the latter are relics— that is, they do not represent a temperate-adapted stock that recently spread north from South Africa.

On the contrary, it seems to us that the distribution pattern could be subject to a very different interpretation. However, what must come first is a phylogenetic analysis of the species, so that relationships can be hypothesized, and thus sense can be made of the different distributions of macropterous and brachypterous taxa, especially those of Section I. Basilewsky (1954a: 22) suggested that occurrence of brachypterous forms of Section I at high altitude is a function of “stenohygrothermy”, for adults of such species live in damp humus in mountains forests. This may be so, but it is no help in understanding phylogenetic relationships of taxa with macropterous and brachypterous adults.

*Material examined.*— Our observations are based on the following material, from collections of the California Academy of Sciences.

*Hystrichopus dorsalis* Thunberg. Three males, three females— South Africa Cape Province George X.28.49 B. Malkin.

*Hystrichopus massaicus* Basilewsky. Two females, from Kenya. Nairobi XII.31.1959, E. S. Ross. 17 mi. SE Nakuru 1900 m; E. S. Ross, R. E. Leech.

*Hystrichopus rufipes* Dejean. Male— South Africa 6mi. NW Port Beaufort 70 m 14.I.1967; E. S. Ross, K. Lorenza.

### Subgenus *Plagiopyga* Boheman, NEW STATUS

Figs. 50, 57, 58, and 85A-B

*Notes about synonymy.*— Basilewsky (1954b: 80) listed *Diaphoroncus* Chaudoir, 1850 as a junior synonym of *Plagiopyga*, and cites as well earlier references to this subgenus.

*Characteristics.*— Basilewsky (1954b: 80-81) provided a useful characterization of adults of this subgenus, contrasting their character states with those of *Hystrichopus (sensu stricto)*. To these we add: stylomere 2 of ovipositor with very short ensiform seta (Fig. 57), and hind wing with oblongum cell larger (Fig. 85A), wedge cell absent (Fig. 85B).

*Notes about classification.*— Ten species are included in this subgenus. Basilewsky (1954a) characterized them, but did not provide an infrageneric arrangement: the species are treated in the sequence in which their names appear in the key (pp. 83-85).

*Notes about habitat.*— Little information is available about this topic. As Basilewsky (1954a: 82) noted, testaceous body color and tendency for reduction in eye size exhibited by

adults indicates that they avoid light. In fact, adults of some species have been collected from caves, rodents' nests, and from under larger rocks. However, the winged condition of adults indicates that dispersal by flight is normal, so that the species are not confined to subterranean situations.

*Geographical distribution.*— This subgenus is predominantly South African, with one species (*H. cyclogonus* Chaudoir) ranging as far north as Tanzania, and four species being known from Zaire, only.

*Notes about phylogeny and zoogeography.*— These topics have not been addressed previously, with reference to this subgenus. Without representative material of all species, we can only make suggestions about a line of investigation to pursue. Because of many shared similarities with members of the surface-dwelling *Pseudomasoreus* and *Hystriichopus*, one can assume that the ancestor of *Plagiopyga* must have been a surface-dweller, also, with average eyes, pectinate tarsal claws (Figs. 52 and 54), and darker color. Extant species whose adults are thus characterized are near the ancestral stock. Reduction of these features probably occurred in more derived stocks that had developed a more apotypic mode of existence. These considerations plus vicariant distribution patterns of species thought to be closely related should provide the clues necessary to reconstruct the phylogeny of the extant species of *Plagiopyga*.

*Material examined.*— Our observations are based on the following material, collected in South Africa.

*H. (Plagiopyga) cymindoides* Péringuey. Three females, - E. Cape Province, Congo Caves X.30.49 B. Malkin (CAS). Three males, female; Stormsriver, W. Humansdorp, 2403415, 4-10.XII. 1981, 525 Peck (from a cave).

*H. (Plagiopyga) chaudoiri* Basilewsky. Female, Queenstown E. T. Wells 1902-19 (BMNH). Female, Natal Estcourt G. A. K. Marshall 1917-55 (BMNH).

### Subtribe CALLEIDINA

We include here two groups of nominal genera that were originally assigned to the Cymindina: *Anomotarus* assemblage— *Anomotarus* Chaudoir, *Lithostrotus* Blackburn, *Dromiotes* Jeannel, and *Cephalotarus* Mateu; and the *Trigonothops* assemblage— *Trigonothops* Macleay, *Phloeocarabus* Macleay, and *Diabaticus* Bates. We add to the latter assemblage *Speotarus* Moore.

By including *Anomotarus* in the Calleidina, we declare the latter name and Anomotarina synonymous. Calleidina is the older name, and is thus valid for this group.

Habu (1967: 117), who established the subtribe Anomotarina, recognized a close relationship of the single included genus with the calleidines, citing as evidence similarity in form of mandibles and female genitalia. Terrestrial modifications of tarsi of adult *Anomotarus* satisfied Habu that this genus should not be included in the Calleidina. However, adults of some calleidine taxa are basically terrestrial, and do not have structurally generalized tarsi that one might expect. We conclude that either tarsi modified for climbing were part of the ground plan of the Calleidina, and were relatively recently lost from some (but not all) groups that became terrestrial secondarily, or that arboreal modifications occurred after calleidines had evolved, and thus were not part of the ground plan. This argument is basic for combining anomotarines and calleidines in a single subtribe.

*Recognition.*— The following features are diagnostic: labrum transverse; without suborbital setae; right mandible with broad, edentate retinacular ridge; maxilla with lacinia and galea sparsely setose; mentum toothed; elytron with umbilical setigerous punctures in continuous line, penultimate puncture not displaced laterally; tarsomeres broad, apical margin of tarsomere 4



89



90



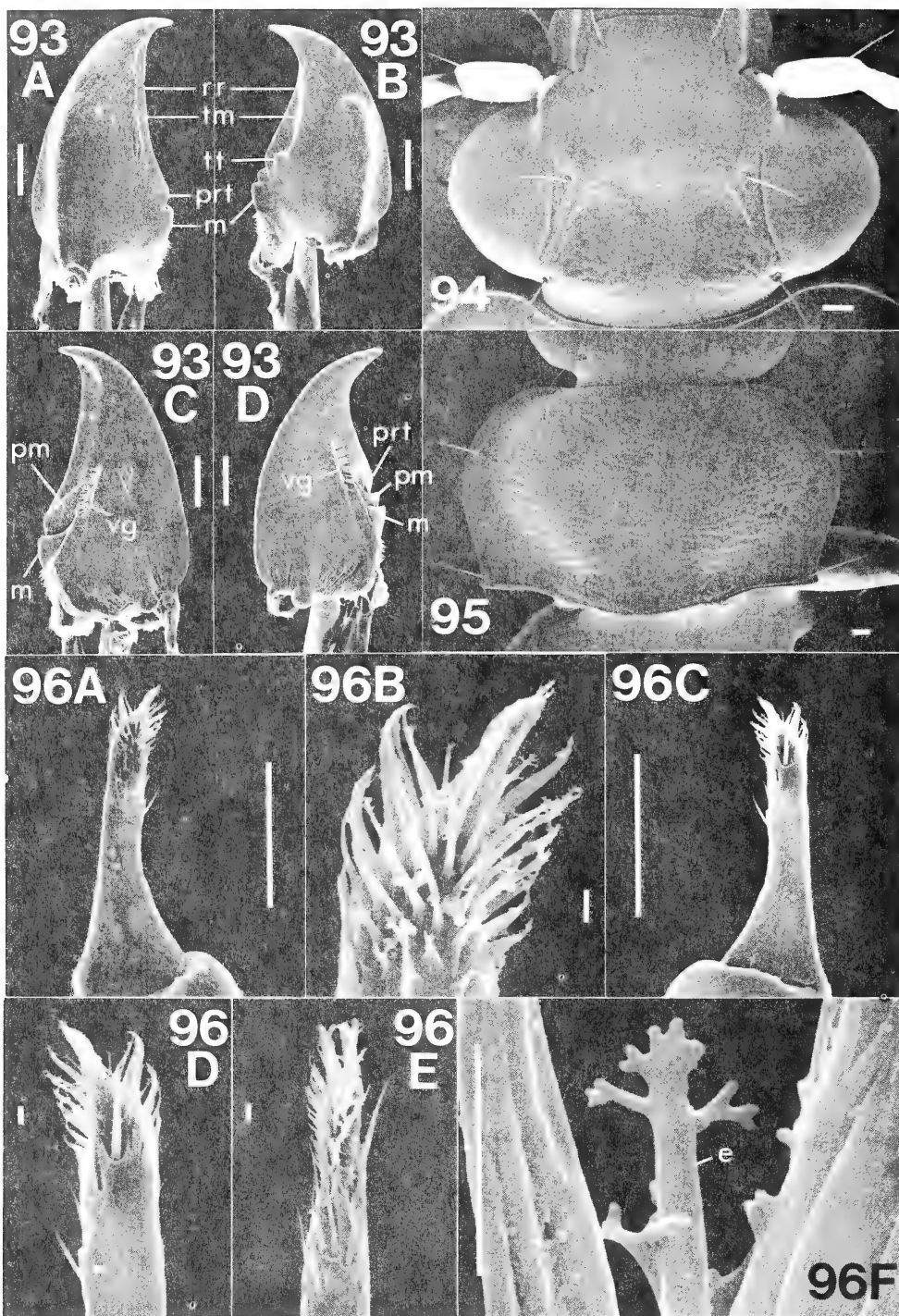
91



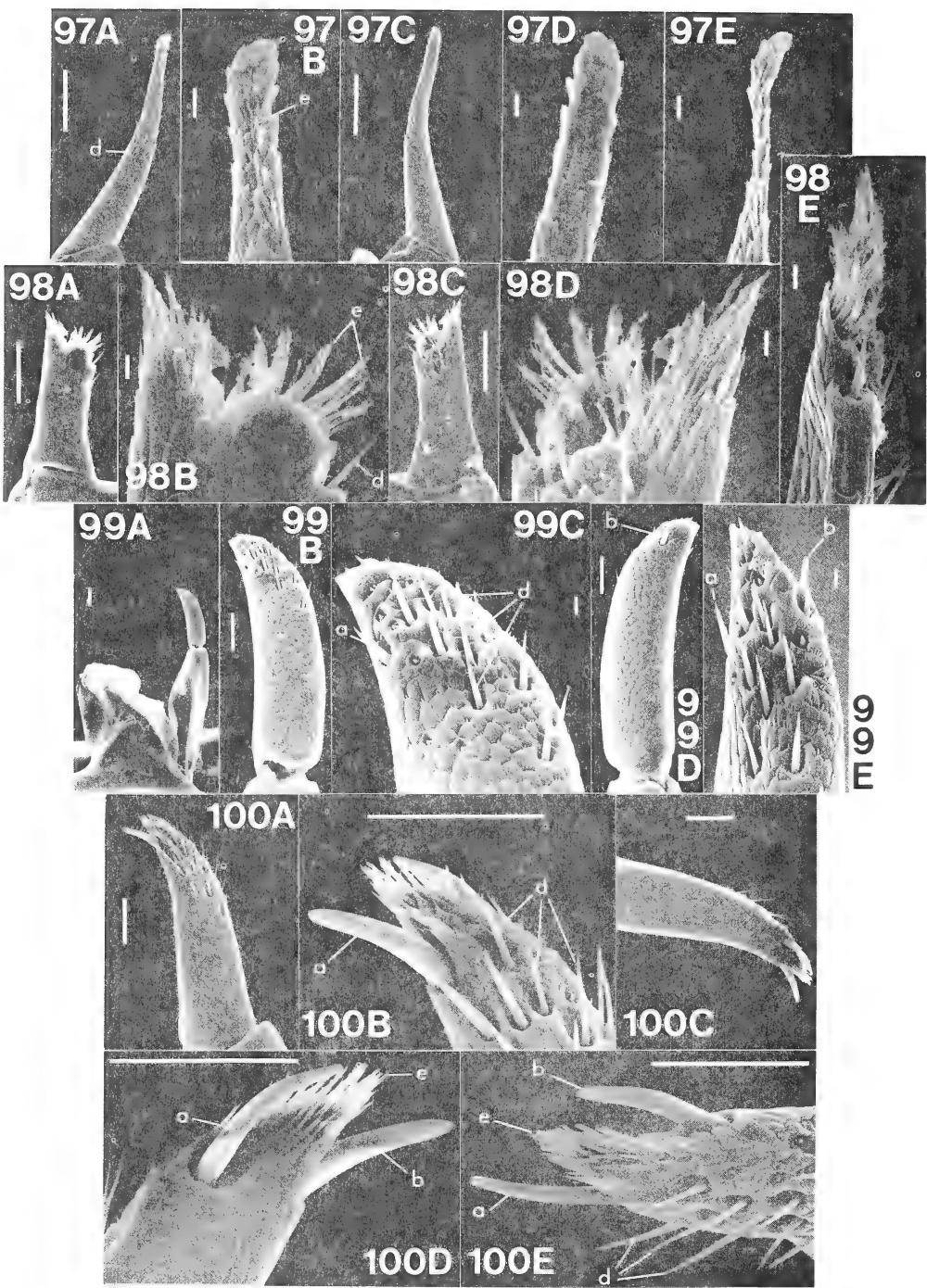
92



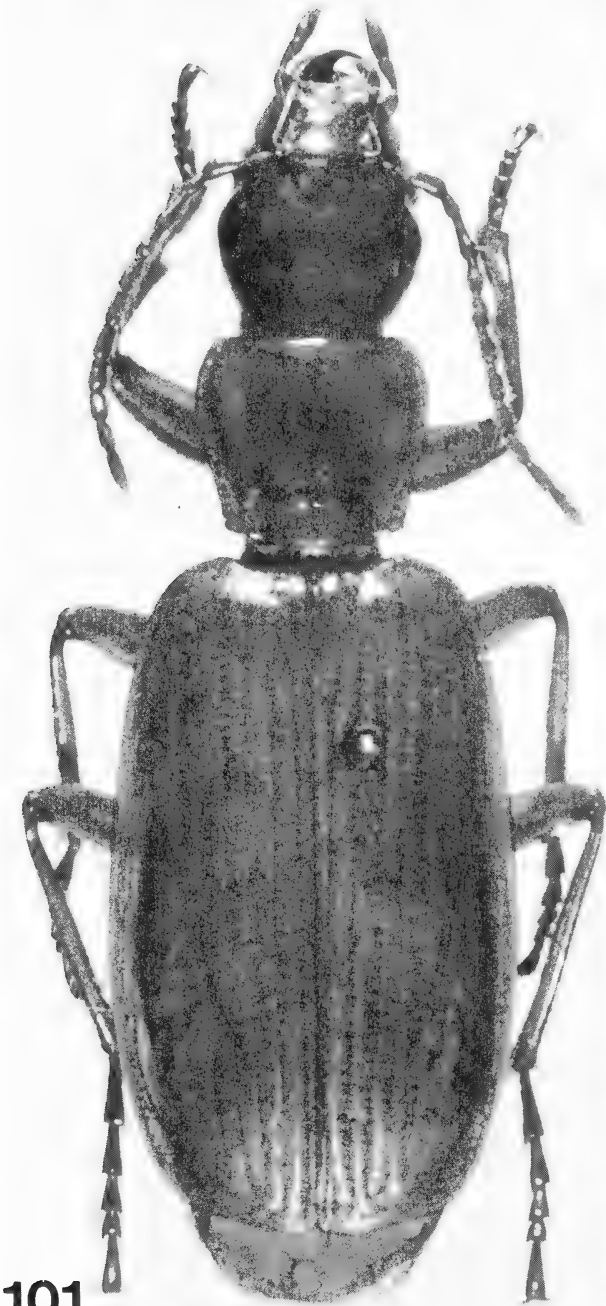
Figs. 89–92. Photographs of Calleidina.—Habitus, dorsal aspect, of specimens of *Trigonothops*: 89, *T. (Diabaticus) australis* (Erichson) (SBL=10.29 mm); 90, *T. (Diabaticus) pauper* (Blackburn) (SBL=6.89 mm); 91, *T. (Abaditicus) collaris* (Blackburn) (SBL=7.88 mm); 92, *T. (Abaditicus) meyeri*, new species (SBL=7.88 mm).



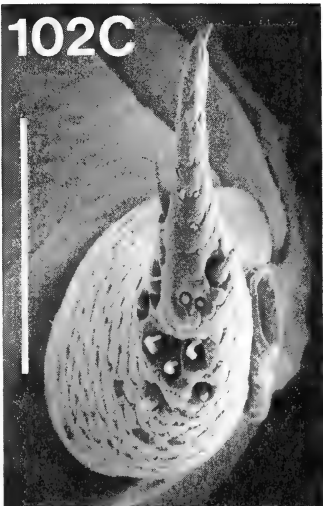
Figs. 93–96. SEM photographs of structures of Calleidina, genus *Trigonothops*.—Fig. 93: *T. (Diabaticus) pauper* Blackburn, mandibles—A and C, left, dorsal and ventral aspects, respectively; B and D, right, dorsal and ventral apical aspects respectively. Figs 94 and 95: *T. (Phloeocarabus) nigricollis* MacLeay, head and pronotum, respectively, dorsal aspect. Fig. 96: *T. (sensu stricto) longiplaga* Chaudoir, left stylomere 2—A, B—lateral aspect; C, D—medial aspect; E—ventral aspect; F—apical branched seta. Scale bars: 93A–96A, and 96C=100  $\mu\text{m}$ , 96B, D, E, F=5  $\mu\text{m}$ . Legend, features of mandibles: m, molar; pm, premolar; prt, posterior retinacular tooth; rr, retinacular ridge; tt, terebral tooth; vg, ventral groove. Legend, stylomere 2: e, branched seta.



Figs. 97–100. SEM photographs of structures of Calleidina, genus *Trigonothops*.—Ovipositors, left stylomeres. Figs. 97 and 98, *T. (Phloeocarabus) nigricollis* Blackburn and *T. (Abaditicus) meyeri*, new species, respectively, stylomere 2: A, B, C, D, and E, lateral, lateral (apical portion); medial, medial (apical portion), and ventral aspect respectively. Fig. 99, *T. (Diabaticus) australis* Erichson: A, valvifer, and stylomeres 1 and 2, lateral aspect; B–E, stylomere 2—B, lateral aspect; C, lateral aspect, apical portion; D, medial aspect; E, ventral aspect. Fig. 100, *T. (Diabaticus) pauper* (Blackburn): A, B, C, D, and E, lateral (apical portion), medial aspect, medial (apical portion), and apico-ventral aspect, respectively. Scale bars: 97A–C, 98A–C, 99B, D, and 100 A–E = 50  $\mu\text{m}$ ; 97B, D, E, 98B, D, E, and 99C and E = 5  $\mu\text{m}$ . Legend: a, lateral ensiform seta; b, medial ensiform seta; d, ventral setae; e, branched apical seta.



101



102C

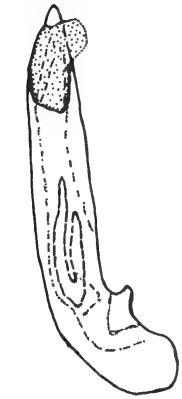


102B

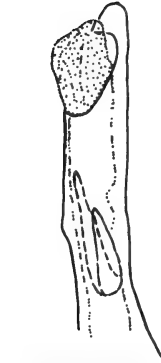


102A

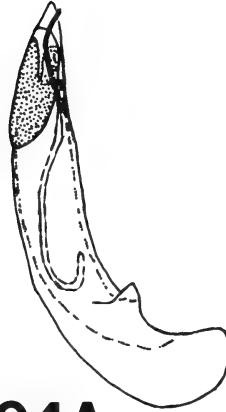
Figs. 101–102. Photographs of Calleidina, *Trigonothops (Speotarus) lucifuga* (Moore).—Fig. 101: habitus, dorsal aspect (SBL=6.98 mm.). Fig. 102: ovipositor, left stylomere 2—A, lateral aspect; B, lateral aspect, apical portion; C, apico-ventral aspect. Scale bars=50  $\mu$ m.



**103A**



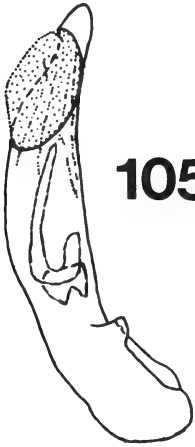
**103B**



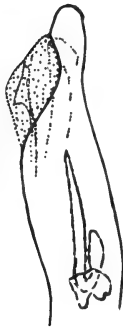
**104A**



**104B**



**105A**



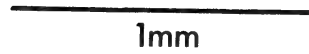
**105B**



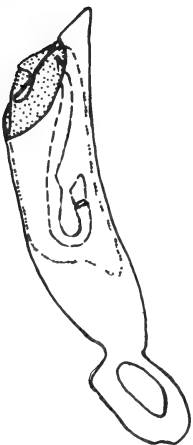
**105C**



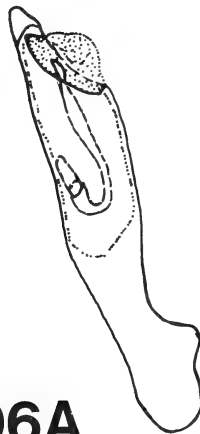
**105D**



1mm



**106A**



**106B**



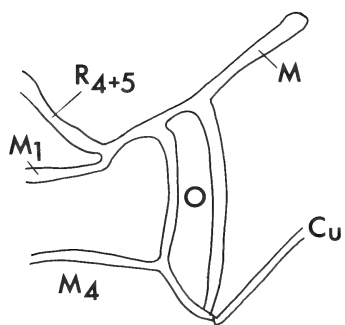
**106C**



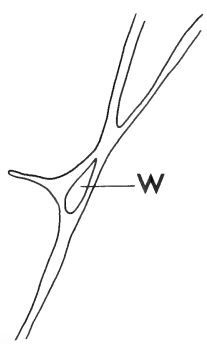
**106D**



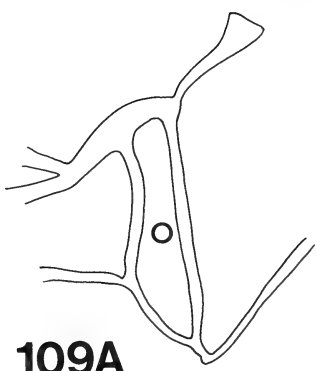
Figs. 103–106. Line drawings of Calleidina, genus *Trigonothops*.—Male genitalia—A and B, median lobe, left lateral and ventral (106B, dorsal) aspects, respectively; C and D, left and right parameres, respectively, ventral aspect, of: 103, *T. (sensu stricto) longiplaga* Chaudoir; 104, *T. (Phloeocarabus) nigricollis* Blackburn; 105, *T. (Abaditicus) meyeri*, new species; 106, *T. (Speotarus) lucifuga* (Moore).



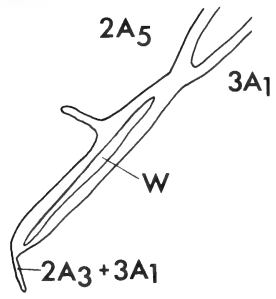
107A



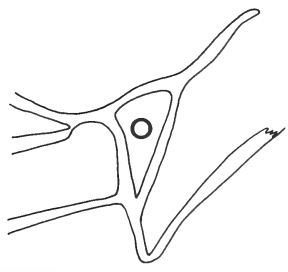
108B



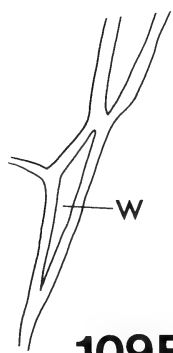
109A



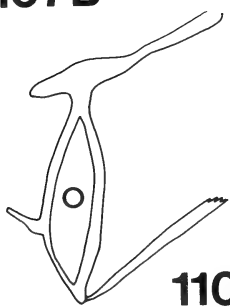
107B



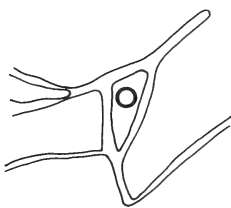
108A



109B



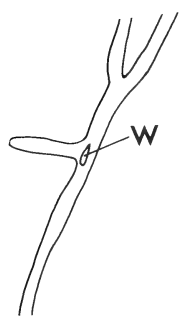
110A



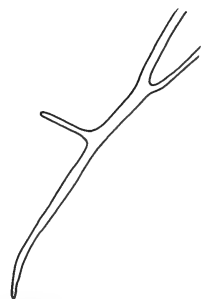
111A



112A



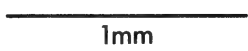
110B



111B



112B



Figs. 107–112. Line drawings of Calleidina.—Wing cells and associated veins—A, oblongum cell, B, wedge cell, respectively, of: 107, *Trigonothops (sensu stricto) longiplaga* Chaudoir; 108, *Anomotarus (sensu stricto) crudelis* Newman; 109, *T. (Phloeocarabus) nigricollis* Blackburn; 110, *T. (Speotarus) lucifuga* (Moore); 111, *Anomotarus (sensu stricto) stigmula* Chaudoir; 112, *A. (Dromiotes) maculipennis* Mateu. Legend: cells—O, oblongum; W, wedge. Veins—A, anal; Cu, Cubitals; M, Media; R, Radius.

sub-truncate or moderately to deeply notched; median lobe of male genitalia with apical orifice hemiopic, on left and ventral side; ovipositor with stylomere 1 glabrous, stylomere 2 approximately cylindrical, tapered, ensiform setae short or absent; apical or preapical portion more or less setose; nematoid setae present or absent.

### The *Trigonothops* assemblage

Figs. 89-92

It is easy to see why *Phloeocarabus* ± and *Diabaticus* were included in the cymindines: tarsi, though moderately broad, are not markedly so, and tarsomere 4 is only notched, without well developed lobes and pads of specialized setae. The tarsi of *Trigonothops* adults are clearly different from those of cymindines, but in other features this group and the former two seem quite close to one another.

It is also easy to see why Moore (1964: 73) placed *Speotarus* (Fig. 101) near *Anomotarus*: in external features, adults of the two groups look much alike. However, the stout tarsi of described *Speotarus* adults suggest a calleidine affinity, and this is borne out by structure of the male genitalia and stylomeres of the ovipositor.

Adults of the four calleidine groups of the *Trigonothops* assemblage exhibit so much similarity to one another that they are here included in a single genus. Furthermore, these groups are confined to the same zoogeographic area, the Australian Region, and this provides additional evidence for inferring close relationship. Additional details are provided below.

### *Trigonothops* MacLeay

*Trigonothops* MacLeay, 1864: 110. GENERITYPE: *Calleida pacifica* Erichson, 1842: 124 (original designation).— Chaudoir, 1877: 221.— Sloane, 1898: 493. 1920: 170.— Csiki, 1932: 1488.— Darlington, 1968: 184.

*Phloeocarabus* MacLeay, 1871: 85. GENERITYPE: *Phloeocarabus mastersi* MacLeay, 1871: 85 (monotypy).— Sloane, 1898: 494-499.— Blackburn, 1901: 112.— Csiki, 1932: 1488.— Darlington, 1968: 183-184 NEW SYNONYMY.

*Notoxena* Chaudoir, 1877: 226. GENERITYPE: *Trigonothops nigricollis* MacLeay, 1864: 111 (monotypy).— Sloane, 1898: 499.— Darlington, 1968: 183-184.

*Diabaticus* Bates, 1878: 324. GENERITYPE: *Plochionus australis* Erichson, 1842: 124 (monotypy).— Csiki, 1932: 1489. NEW SYNONYMY.

*Speotarus* Moore, 1964: 71. GENERITYPE: *Speotarus lucifugus* Moore, 1964: 73 (original designation).— Matthews, 1980: 10. NEW SYNONYMY.

*Abaditicus*, new subgenus. GENERITYPE: *Diabaticus collaris* Blackburn, 1901: 111 (here designated).

*Notes about classification.*— Inclusion of these taxa in a single genus makes the latter difficult to define in terms of external features. However, we feel confident that this assemblage is monophyletic, and we feel that it is more important to emphasize relationships inferred from complex internal structures than to emphasize differences, which, though easily perceived, seem of less importance. Attention is thus drawn to an underlying unity, and we hope that this will stimulate future workers on Australian carabids to undertake study of the group as a whole.

To draw attention to divergence within *Trigonothops*, we recognize four previously named assemblages as subgenera: *Trigonothops* (*sensu stricto*), *Phloeocarabus*, *Diabaticus*, and *Speotarus*. However, the nominal genus *Diabaticus* seems to be paraphyletic, including two species that are less closely related to its type, *D. australis* Erichson, than to other group of *Trigonothops*. Therefore, we erect a fifth subgenus, *Abaditicus*, no previously published names being available.

The generitype of *Notoxena* Chaudoir is included in *Phloeocarabus* ±. Chaudoir (1877: 226), when he described *Notoxena*, did not cite MacLeay (1871). Hence, he must have been unaware that a genus had already been proposed that would include *T. nigricollis*.

**Descriptive notes.**— To the characterization of *Trigonothops* by Darlington (1968: 183), we add the following. Adults with eyes large, prominently bulged, temples small (Fig. 94), or only slightly convex, with temples well developed (Fig. 101). Tarsomere 4 notched or bilobed; tarsal claws pectinate or smooth. Male genitalia with median lobe hemiopic, internal sac with large flagellum- like sclerite (Figs. 103-106). Ovipositor with stylomere 1 asetose, stylomere 2 cylindrical, ensiform setae two or absent, ventral surface setose; apical portion extended and attenuate (Figs. 97A, C) or not (Figs. 98A, C).

**Way of life.**— Adults of *Trigonothops* (*sensu stricto*), *Phloeocarabus*, ± and *Abaditicus* are arboreal. We do not know where adults of *Diabaticus* live, but we assume that they spend at least part of their lives on trees. Adults of *Speotarus* are known only from caves.

**Evolutionary trends.**— If, as we believe, calleidines are basically arboreal, then the arboreal groups of *Trigonothops* are likely to be closer to the ancestral stock of the genus, with the cave-inhabiting *Speotarus* being the more remote. If this is correct, the smooth tarsal claws and rather flattened eyes of adults of *Speotarus* are probably apotypic, denticles having been lost from the ancestral stock of this subgenus, and the compound eyes reduced.

### Key to Subgenera of *Trigonothops*

- 1 (0) Tarsal claws smooth; eyes slightly convex, temples large (Fig. 101); pronotum with narrow lateral grooves, only slightly transverse (Fig. 101) ..... *Speotarus* Moore, p. 191
- 1' Tarsal claws pectinate; eyes markedly convex and bulged, temples small (Figs. 89-92, and 94); pronotum with wider lateral grooves, more transverse (Figs. 89-92, and 95) ..... 2
- 2 (1') Tarsomere 4 cleft apically, with pair of large lobes, ventrally with modified setae ..... *Trigonothops* (*sensu stricto*), p. 188
- 2' Tarsomere 4 notched apically, lobes short, without modified vestiture ventrally ..... 3
- 3 (2') Head with pair of distinct longitudinally directed lateral ridges, especially prominent between supraorbital setigerous punctures, and extended to posterior pair (Fig. 94); eyes very large, entire lateral area of head occupied; pronotum very broad, basal margin distinctly lobed (Fig. 95) ..... *Phloeocarabus* MacLeay, p. 188
- 3' Head without longitudinally directed ridges, or these shorter, not extended to posterior pair of supraorbital setigerous punctures; temples short, eyes average in size (Figs. 89-92), though prominent; pronotum narrower, more elongate, basal margin convex, but not distinctly lobed ..... 4
- 4 (3') Head sharply constricted posteriorly, in form of neck (Figs. 91, 92); elytron with microsculpture meshes isodiametric, not transverse ..... *Abaditicus*, new subgenus, p. 189
- 4' Head not sharply constricted in form of neck (Figs. 89, 90); elytron with microsculpture meshes transverse ..... *Diabaticus* Bates, p. 188

Subgenus *Trigonothops* (*sensu stricto*), NEW STATUS

Figs. 96A-F, 103A-B and 107A-B

**Descriptive notes.**— To Darlington's (1968: 184-185) characterization of this taxon, we add the following, based on study of 12 specimens (CAS) of two species, from various localities in Queensland and New South Wales. Hind wing with average oblongum cell, and wedge cell long, narrow (Figs. 107A, B) or both cells reduced (Figs. 108A, B). The basal portion of the flagellar sclerite of the internal sac is almost as long as the main part (Figs. 103A, B), that is, this structure is relatively short. Stylomere 2 of the ovipositor is as follows: form as in Figs. 96A, C, base broad, tapered markedly about half length, then parallel-sided; apex blunt; microsculpture with meshes distinct at base, isodiametric, each scale with acuminate tip; in apical 0.50, meshes elongate microlines shallow; apical 0.33 with few spines (Figs. 96D, E), one large ensiform seta dorso-laterally (Fig. 96D), and apical 0.20 with branched (Figs. 96B and F) and unbranched long setae extended from microscales.

Subgenus *Phloeocarabus* MacLeay NEW STATUS

Figs. 94, 95, 97A-E, 104A-B, and 109A-B

±

**Descriptive notes.**— To Darlington's (1968: 183) characterization of this taxon, we add the following, based on examination of his series of *T. nigricollis*, from various localities in New Guinea and Australia. Wing with cells large (Figs. 109A, B). The internal sac of the male genitalia contains a large reverse "J" shaped sclerite (Figs. 104A, B). Stylomere 2 of the ovipositor as in Figs. 97A-E, elongate, tapered gradually to narrow apex; microsculpture rather irregular, microlines fine, meshes isodiametric basally, elongate apically, (Figs. 97B, C); few setae mainly on lateral and dorsal surfaces, about half way between base and apex, without ensiform setae; short seta-like projections extended from microscales in apical 0.20 (Figs. 97B, D, and E).

Subgenus *Diabaticus* Bates, NEW STATUS

Figs. 89, 90, 93A-D, 99A-E and 100D-E

Having had the opportunity to see specimens of the three described species that were previously included, and of a fourth related but undescribed species, and having reached the conclusion that two subgenera are represented rather than one, it seems appropriate to offer a more extended analysis of this complex.

Structures that seem best to show relationships in *Trigonothops* are male genitalia and ovipositor. Unfortunately, we have both males and females of only one species of the *Diabaticus* complex, *T. meyeri*, new species. *T. australis* (Erichson) and *T. pauper* (Blackburn) are represented by females, only; and *T. collaris*, by a single male. However, because of the general pattern that we perceive, we feel certain that the missing pieces of evidence will fit in, when they are eventually found.

Stylomere 2 of ovipositors of *T. australis* (Fig. 99) and *T. pauper* (Fig. 100) is markedly different in form and sculpture from stylomere 2 of a *T. meyeri* female (Fig. 98). The latter stylomere is more like that of *Trigonothops* (*sensu stricto*) and *Phloeocarabus* females. We think it likely that *T. australis* and *T. pauper* females exhibit the plesiotypic form, and that the other forms are apotypic.

With *T. meyeri*, we group *T. collaris* Blackburn because of striking similarities in the genitalia and in form of head.

**Descriptive notes.**— Form as in Figs 89 and 90.

Color: body piceous, appendages rufous, elytra concolorous. Microsculpture and luster: dorsum of head (including labrum and clypeus) with meshes isodiametric, surface dull; pronotum with meshes transverse, surface shining, but not iridescent; lateral and ventral thoracic sclerites (including mesepisterna) with meshes transverse; abdominal sterna with meshes transverse, surface iridescent; scutellum with meshes isodiametric. Dorsal surface glabrous (except standard fixed setae), or sparsely setose. Pronotum subcordate, sides sinuate posteriorly, margins broadly curved upward; posterior angles

approximately right. Ovipositor: stylomere 2 as in Figs. 99 and 100, blade-like, apical 0.33 straight (Fig. 99C), or slightly twisted (Fig. 100E); microsculpture predominantly of isodiametric meshes (Figs. 99D-E), elongate on apico-medial surface of *D. pauper* (Fig. 100D), lines deep, each scale with acuminate tip; apico-dorsal 0.33 with 15-20 trichoid setae, two ensiform setae pre-apically, one lateral, one medial, short (Fig. 99E), or longer (Fig. 100E); apex with (Figs. 100D, E) or without (Figs. 99C, E) fine setae extended from microscales.

**Geographical distribution.**— This subgenus is known from Tasmania and southeastern Australia, only.

### Key to Species of Subgenus *Diabaticus*

- 1 (0) Dorsum of body and dorsal surfaces of tarsomeres generally punctate and setose; metepisternum short, with anterior and lateral margins subequal . . . . . *T. (Diabaticus) pauper*, Blackburn, p. 189
- 1' Dorsum of body and dorsal surfaces of tarsomeres glabrous, generally impunctate; metepisternum long, lateral margin longer than width at anterior margin . . . . . *T. (Diabaticus) australis* (Erickson), p. 189

### *Trigonothops (Diabaticus) australis* (Erickson), NEW COMBINATION Figs. 89 and 99A-E

*Plochionus australis* Erickson, 1842; 124.

*Diabaticus australis*; Bates, 1878: 324.— Blackburn, 1901: 17.— Csiki, 1932: 1489.

**Descriptive notes.**— Standardized Body Length of two females: 8.60 and 8.96 mm. Values for  $V_{wm}/H_w$  0.59 and 0.62. Lateral margins of pronotum only slightly elevated; broad lateral grooves markedly narrowed near anterior setigerous punctures, these in bottom of lateral grooves, clearly removed from margin. Elytron with basal ridge complete, extended from humerus to suture, near scutellum.

Bates (1878: 325) noted the superficial similarity in body form between adults of this species and those of *Cymindis (Pinacodera) punctigera* (LeConte).

**Specimens examined.**— Two females (BMNH), both determined by T.G. Sloane: one labelled Hobart, 91-88 [ovipositor dissected]; the other, V D Ld 77- 19; 146 [abdomen lacking].

### *Trigonothops (Diabaticus) pauper* (Blackburn), NEW COMBINATION Figs. 90 and 100A-E

*Diabaticus pauper* Blackburn, 1901: 111. HOLOTYPE female, labelled: Tazm [red print] T; Type [circular label, ringed with red]; Blackburn Coll 1910- 236; *Diabaticus pauper*, Blackb. [handwritten] (BMNH).— Csiki, 1932: 1489.

**Descriptive notes.**— Form as in Fig. 90. Standardized Body Length (five females): 5.60-(6.17)- 6.76 mm. Range of values for ratio width of neck to width of head: 0.53-0.65. Dorsal surface of frons and pronotum laterally rugulose, and elytral striae deeper than in adults of *T. australis*. Pronotum more narrowed posteriorly, and lateral margins more elevated; lateral margins of elytra crenulate; humeri narrowed (associated with wing loss and reduction of metathorax), and marginal ridge terminated near base of interneur 4. Ovipositor with stylomere 2 as in Figs. 100A-E.

**Geographical distribution.**— This species is known from Tasmania, only.

**Material examined.**— In addition to the holotype, we have seen four females (BMNH): two labelled Franklin, Tasmania, 91- 88; and two labelled Hobart, 91- 88.

### *Abaditicus*, new subgenus Figs. 91, 92, 98A-E, and 105A-D

This taxon is established to include *Diabaticus collaris* (Blackburn) and *Trigonothops meyeri*, new species.

*Derivation of subgeneric name.*— This is an anagram of *Diabaticus*, the name of the group to which *T. collaris* was originally assigned.

*Recognition.*— The markedly constricted posterior part of the head (Figs. 91 and 92) is sufficient to distinguish adults from those of other subgenera of *Trigonothops*. Additionally, the basal ridge of the elytron is extended only to the base of interneur 3; females have stylomere 2 of the ovipositor short and stout and without ensiform setae (Fig. 98); and males have a moderately long sclerite (Fig. 105B) in the internal sac.

*Descriptive notes.*— Form as in Figs. 91 and 92.

Color: body and appendages rufous; elytra concolorous (rufous) or bicolored (Fig. 92). Microsculpture and luster: dorsum of head (including labrum and clypeus) with meshes isodiametric, surface dull; pronotum with meshes transverse, surface shining but not iridescent; most lateral and ventral thoracic sclerites with meshes transverse, mesepisternum with meshes isodiametric; abdominal sterna with meshes transverse, surface iridescent. Dorsal surface glabrous (except standard fixed setae). Pronotum subcordate, sides sinuate posteriorly, lateral margins broadly curves upward; posterior angles approximately right. Elytron with basal ridge terminated near base of interneur 3, not extended to sutural margin. Internal sac of male genitalia with large, reverse "J"-shaped sclerite (Fig. 105B).

Stylomere 2 of ovipositor as in Figs. 98A-E, short, broad, constricted slightly medially, broadened apically, apical margin very broad (Fig. 98B). Microsculpture meshes isodiametric or slightly elongate, microlines generally distinct, scales without acuminate tips. Apical 0.25 with setae on lateral and dorsal surface, but not on medial surface, without ensiform setae; apex with long setae extended from microscscales.

*Geographical distribution.*— This subgenus is known from southeastern Australia (Victoria), only.

*Relationships.*— We believe *Abaditicus* is the primitive sister group of the subgenus *Phloeocarabus*, ± based on inferred transformation series in armature of the internal sac, and details of stylomere 2.

#### Key to Species of Subgenus *Abaditicus*

- 1 (0) Elytra concolorous, rufo-piceous ..... *T. (Abaditicus) collaris* (Blackburn), p. 190
- 1' Elytron sharply bicolored, most of surface piceous, with apex and extensive area of disc rufous (Fig. 92) ..... *T. (Abaditicus) meyeri*, new species, p. 190

#### *Trigonothops (Abaditicus) collaris* (Blackburn), NEW COMBINATION

Fig. 91

*Diabaticus collaris* Blackburn, 1901: 111. HOLOTYPE male labelled: 6954 H. Wick [red print] T; Type [circular, ringed with red]; Blackburn coll 1910- 236; *Diabaticus collaris* Blackb. [handwritten] (BMNH).— Csiki, 1932: 1489.

*Descriptive notes.*— Form as in Fig. 91. Standardized Body Length 6.88 mm. Value for ratio width of neck to maximum width of head 0.49. Pronotum with lateral grooves broader than in adults of *T. australis*, and hardly narrowed anteriorly; anterior pair of setigerous punctures nearly marginal. Median lobe as in Fig. 105, internal sac with reverse "J"-shaped sclerite.

*Material examined.*— Holotype, only.

#### *Trigonothops (Abaditicus) meyeri*, new species

Figs. 92, 98A-E, and 105A-E

*Type material.*— HOLOTYPE male, labelled: Woodhouse Ck., Nunniong Plt. Vic. 16.5.66. P. Meyer; under bark of *E. delegatensis* (CSIRO). Three paratypes, from the same locality:



collected on May 16- female (CAS); collected on May 26- male (BMNH); female (MCZ).

*Derivation of specific epithet.*— From the surname of the collector, Peter A. Meyer, Heidelberg, Victoria, Australia, to whom the senior author is grateful for the gift of these and other specimens.

*Recognition.*— This is the only known species of *Abaditicus* whose adults have spotted elytra.

*Description.*— Character states of subgenus, and the following. Form as in Fig. 92. Standardized Body Length, males 6.9- 7.12 mm., females 6.88- 7.08 mm. Body form *Calleida*- like. Neck evident (W vertex min./Hw males 0.52- 0.53, female 0.52. Hw/Pl- males, 0.87- 0.89, females, 0.86- 0.92; Pl/El- males, 0.300- 0.32, females 0.29- 0.30.

Color. Appendages and body except elytra rufous; elytron with following rufous- epipleura, lateral groove, apical 0.16, and irregular discal area from interval 2 to 6, extended to humerus on interval 5; following black- interval 1, in basal 0.84, triangular area near scutellum, transverse band in apical 0.33, and intervals 7- 9 throughout most of length.

Microsculpture. As described for subgenus. Surface slightly shining, pronotum more so than head or elytra.

Fixed setae. Average for *Calleidina*: both pairs of pronotal setae on lateral margins.

Head. Frons and anterior part of vertex depressed. Frontal impressions extended diagonally to anterior pair of supraorbital setigerous punctures. Eyes average for subgenus; occipital area markedly constricted. Mouthparts average, including mental tooth, axiniform ultimate labial palpomeres, and bisetose penultimate palpomeres.

Pronotum. Moderately transverse, anterior margin shallowly concave, posterior margin convex, but not clearly lobed; lateral margins distinctly to slightly sinuate; anterior angles broadly rounded, posterior angles about right; lateral margins elevated, more broadly so posteriorly; disc broad, only slightly convex medially; median longitudinal impression sharply delimited, extended from near anterior to near posterior margin; posterior-lateral impressions indistinct, shallow, broadly continuous with broad lateral grooves.

Elytra. Humeri broadly rounded, apical margin subtruncate; basal ridge terminated near base of interneur 3, not extended to parascutellar setigerous puncture; interneurs shallow, intervals hardly convex.

Male genitalia. As in Figs. 105A-D, average for *Calleidina*.

Ovipositor. Stylocere 2 as in Figs. 98A-E.

*Notes about habitat.*— According to the labels, specimens in the type series were collected under bark of a eucalyptus tree. Probably, then, this species is arboreal. Interestingly the color pattern of these specimens is like that of many arboreal Australian lebiines (for example, *Trigonothops longiplaga Chaudoir*). Darlington (1971: 250-251) suggested that mimicry might be involved as an explanation for similarity in color pattern exhibited by some tree trunk-inhabiting lebiines, though he did not refer specifically to the pattern characteristic of *T. meyeri*. This suggestion seems reasonable to us, and we extend it in terms of Müllerian mimicry, to the many groups of Australian lebiines that are colored like adults of *T. meyeri*. Erwin (1978 and 1979) discussed tests of defense mechanisms that showed them to be powerful for adults of *Agra* and other lebiines. This is supporting evidence that this group of insects has the necessary equipment to form the basis for development of complexes of protected mimics.

*Geographical distribution.*— This species is known only from the type locality, which is in the general range of the previously described species of *Abaditicus*.

*Phylogenetic relationships.*— Adults of this species share with those of *T. collaris* a head with constricted occipital area, and elytra with basal ridges incomplete. These synapotypic features satisfy us that these two species are more closely related to one another than to the other known species of *Trigonothops*.

#### Subgenus *Speotarus* Moore, new status Figs. 101, 102A-C, 106A-D, and 110A-B

*Descriptive notes.*— The following details are added to the original description of *Speotarus* (Moore, 1964: 91). These notes are based on two specimens of *T. lucifugus* Moore, 1964: male, Cocklebidy Cave, Eucla Basin, S. Australia, bat piles 12.1.66, J. Lowrey; female, bat cave, Naracoorte, 9 Mar, 1963, E. Hamilton-Smith.

Habitus as in Fig. 101. Standardized Body Length, male 6.86 mm., female, 7.06 mm.

Microsculpture. Dorsum of clypeus and anterior part of frons smooth, microlines not evident, vertex with meshes isodiametric, microlines shallow; thoracic and abdominal sclerites, and elytra with meshes transverse. Surface generally shining, especially head.

Head. Eyes though extensive in area, only slightly convex, not protuberant (Fig. 101).

Pronotum. Narrow, slightly transverse, lateral grooves narrower than in *Trigonothops (sensu stricto)* adults.

Legs. Anterior and middle femora with more setae than usual, posterior face of middle femur with more than 12 setae.

Wings. Completely developed, not reduced. Oblongum cell fusiform (Fig. 110A), wedge cell very small (Fig. 110B).

Median lobe of male genitalia hemiopic, apical orifice to left and ventrad (Figs. 106A, B). Internal sac with reverse "J"-shaped sclerite, and small sclerite. Parameres as in Figs. 106C, D.

Ovipositor (Figs. 102A-C). Stylomere 1 asetose. Stylomere 2 elongate, apical portion tapered, preapically with pair of ensiform setae (one lateral, one medial), and several trichoid setae on ventral surface. Microsculpture with sculpticells elongate, each with small spine directed apically; microsculpture otherwise simple.

*Notes about way of life.*— Also included in subgenus *Speotarus* is a second species, *T. princeps* (Moore, 1964). Both species are known only from caves. Although pale color of integument and rather reduced eyes are cavernicolous adaptations, the normally proportioned metathorax and rather long wings of *Speotarus* adults suggest that they are not troglobitic. Moore (*in litt.*) advised us: "the species are undoubtedly troglaphiles (guanophiles) and are plentiful in certain caves, notably on the Nullarbor Plain, where there are no trees and no surface litter." Further, he stated that the beetles have not been found in the course of extensive surveys of the litter-fauna, in southern Australia. This counters our first thought that habitus of the beetles suggests adaptation to life in deep litter.

Moore (personal communication) advises us that additional specimens of *Speotarus* have been found in additional caves. These beetles exhibit some differences from the previously described species, and may represent undescribed taxa.

*Evolutionary considerations.*— In the letter cited above, Moore advanced an hypothesis to explain the cave-inhabiting way of life of a stock that might have been arboreal. He suggested that the extant species of *Speotarus* were derived from tree-dwelling calleidines that took up life in tree-roosting bat colonies, and became adapted to living in association with guano. It would be but a rather short evolutionary step from that stage to life in caves inhabited by bats. As he noted, support for this hypothesis would come from discovery of *Speotarus* specimens in association with arboreal bats. We think that Dr. Moore's idea has merit, and hope that he succeeds in his quest for confirmatory evidence.

### The *Anomotarus* assemblage

For reasons stated below, we combine the named genera of this complex in a single genus, *Anomotarus* Chaudoir. Further, we have considered seriously the possibility of a close relationship between *Anomotarus (sensu lato)* and *Trigonothops (sensu lato)*. However, we were unable to identify synapotypic features to support this alliance.

#### *Anomotarus* Chaudoir

Figs. 108A, B, and 113-117

*Anomotarus* Chaudoir, 1875: 48. GENERITYPE: *Anomotarus olivaceus* Chaudoir, 1875: 48 (monotypy).— Sloane, 1898: 494.— 1917: 435.— 1920: 170.— Csiki, 1932: 1492- 1493.— Jedlička, 1963: 300, 450.— Moore, 1964: 73.— Habu, 1967: 118- 121.— Darlington, 1968: 186- 191.— Mateu, 1970b: 148.— 1972: 44.— Moore, 1967a: 183- 184.

*Uvea* Fauvel, 1881: CXVIII. GENERITYPE: *Cymindis stigma* Chaudoir, 1852: 57 (monotypy).

*Nototarus* Chaudoir, 1875: 19. GENERITYPE: *Nototarus australis* Chaudoir, 1875: 19 (monotypy).— Sloane, 1898: 494.— Csiki, 1932: 1492.— Moore, 1963: 442.— 1967b: 442-445.— Darlington, 1968: 185- 186. NEW SYNONYMY.

*Lithostrotus* Blackburn, 1894: 200. GENERITYPE: *L. coerulescens* Blackburn, 1894: 200 (monotypy).— Sloane, 1898: 494.— Csiki, 1932: 1492. NEW SYNONYMY.

*Lestianthus* Sloane, 1894: 451. GENERITYPE: *Lestianthus sculpturatus* Sloane, 1894: 452 (monotypy) (= *Lithostrotus coerulescens* Blackburn).

*Dromiotes* Jeannel, 1949: 914. GENERITYPE: *Lebia stigmula* Fairmaire, 1901: 126 (= *A. jeanneli* Mateu, 1972: 47, not *A. stigmula* Chaudoir, 1852: 57) (original designation).— Mateu, 1972: 44.

*Cephalotarus* Mateu, 1970b: 150. GENERITYPE: *Cephalotarus maculipennis* Mateu, 1970b: 151 (monotypy).— 1972: 46.

*Notes about names and classification.*— By inclusion in *Anomotarus* of *Dromiotes*, the type species of the latter (*Lebia stigmula* Fairmaire, 1901) becomes a secondary junior homonym of *A. (sensu stricto) stigmula* (Chaudoir, 1852). For the name *L. stigmula* Fairmaire, therefore, Mateu (1972: 94) proposed the new name *Anomotarus (Dromiotes) jeanneli*. Character states diagnostic for these taxa seem too slight and too few to warrant ranking as genera. Thus, we think it best to include all of the species in a single genus. However, we also think it desirable to indicate the pattern of divergence in the genus by recognition of three subgenera: *Dromiotes* Jeannel; *Anomotarus (sensu stricto)*; and *Nototarus* Chaudoir (including *Lithostrotus* Blackburn).

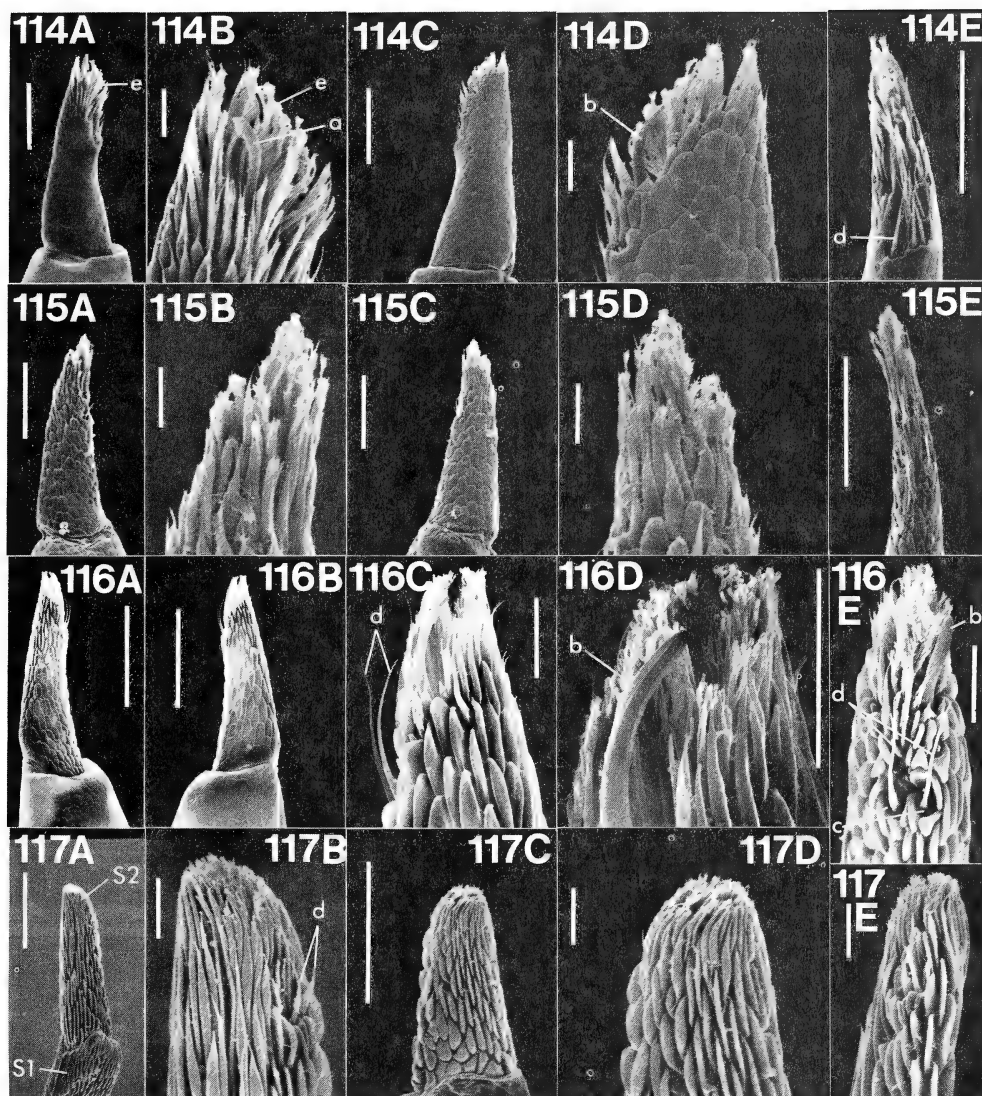
Justification of synonymy of *Nototarus* and *Lithostrotus* is required. Distinctive features of adults of *Lithostrotus* are: dorsal integument metallic blue, surface densely, coarsely punctate (Fig. 113), and setose, with microsculpture generally effaced; eyes small, temples large; Pronotum (Fig. 113) with very sharp posterior angles and sharply defined basal lobe. Our material of *Nototarus* includes adults of eight species (mostly unnamed). None exhibit metallic color, but two have a pattern of punctuation similar to that of *Lithostrotus*, with the pronotum similar in form, and eyes similarly reduced. Adults of two species are less coarsely punctate, and are glabrous; the others are impunctate, and have rather larger eyes. In brief, the differences are bridged between the *Lithostrotus* adults and those of the more typical *Nototarus* species. Thus, a transformation series seems to be indicated, with one end represented by *Lithostrotus*. It will no doubt be desirable to recognize species groups, in conjunction with revision of the species of this subgenus.

#### Key to Subgenera of *Anomotarus (sensu lato)*

- 1 (0) Mentum toothed. Metepisternum elongate, lateral margin longer than width at anterior margin. Elytron with microsculpture meshes more or less transverse. Eyes large. Internal sac with or without sclerite. Stylomere 2 of ovipositor with sculpticells flat (Figs. 114 and 115) ..... 2
- 1' Mentum edentate. Metepisternum short, lateral and anterior margins subequal. Wings reduced. Elytron without microlines, or meshes transverse. Eyes reduced, though head large. Internal sac with large sclerite. Stylomere 2 of ovipositor with surface rugose, sculpticells raised as keels; pair of long slender, curved setae near apex (Fig. 116D) or not (Fig. 117D) ..... Subgenus *Nototarus* Chaudoir.
- 2 (1') Wing with oblongum cell broad (Fig. 112A), wedge cell small (Fig. 112B). Internal sac of male with well developed sclerites, flagellum-like or not. Stylomere 2 without long, curved setae (Figs. 115A-E). Species Afrotropical .. Subgenus *Dromiotes* Jeannel.
- 2' Wing with oblongum cell narrow, wedge cell absent (Figs. 111A, B); or small (Fig. 108B). Internal sac without sclerites. Stylomere 2 of ovipositor with long, slender, curved setae (Figs. 114B and D). Species Oriental or Australian ..... *Anomotarus (sensu stricto)*.



Fig. 113. Photograph of Calleidina.— *Anomotarus (Nototarus) coerulescens* (Blackburn), habitus, dorsal aspect (SBL=4.89 mm.).



Figs. 114–117. SEM photographs of Calleidina, genus *Anomotarus*.—Ovipositors, left stylomeres 1 and 2, or 2, only, A, B, C, D, and E—lateral, lateral (apical portion), medial, medial (apical portion), and apico-ventral aspects, respectively, of: 114, *A. (sensu stricto) stigmula* Chaudoir; 115 *A. (Dromiotes) maculipennis* Mateu; 116, *A. (Nototarus) coerulescens* (Blackburn); 117, *A. (N.) tumidiceps* (Blackburn). Scale bars: 114A, C, E, 115A, C, E, 116A, B, and 117A, C=50  $\mu$ m; 114B, D, 115B, D, 116C, D, E, and 117B, D, E=10  $\mu$ m. Legend: a, lateral ensiform seta; b, medial ensiform seta; c, sensory furrow; d, nematoid setae; e, branched apical seta; S1, stylomere 1; S2, stylomere 2.

Darlington (1968: 185-187) provided useful descriptions of *Anomotarus* and *Nototarus*, to which we add that species with brachypterous members and with mental tooth probably belong to *Anomotarus* (*sensu stricto*). Hence, both of these subgenera have brachypterous members. Moore (1964: 73) suggested that it may be necessary to erect a new genus to include several species that seem to have adult characteristics similar to those of *A. tumidiceps* Blackburn.

The seeming scarcity of specimens of *A. coerulescens* makes it desirable to have a detailed account available, for the benefit of workers on Australian carabids.

*Anomotarus* (*Nototarus*) *coerulescens* Blackburn, NEW COMBINATION

Figs. 113, and 116A-E

*Lithostrotus coerulescens* Blackburn, 1894: 200. HOLOTYPE female, labelled: 5274 Vict [red print] T; Type [circular, ringed with red]; Blackburn coll 1910- 236; *Lithostrotus coerulescens* Blackb [handwritten] (BMNH).

*Lestianthus sculpturatus* Sloane, 1894: 451 (type not seen).— 1898: 494.

*Lithostrotus planior* Blackburn, 362. HOLOTYPE female, labelled: B7 MCS 7755 [red print] T; Type HT [circular, ringed with red]; Australia Blackburn coll BM 1910- 236; *Lithostrotus latior* Blackb [handwritten]; This must be the type of *planior*. The name *latior* was evidently written in error. No such name as *latior* has been published. A.M. Lea 6/9/12 [handwritten] (BMNH). TYPE LOCALITY: Australia New South Wales, Blue Mountains, 3000 feet.— Lea, 1912: xxviii. NEW SYNONYMY.

*Notes about synonymy.*— We have seen the above-listed holotypes. They are so similar to one another that it seems they must be conspecific, and we regard them as such.

*Recognition.*— The following combination of character states sets adults of this species apart from others included in *Anomotarus*: dorsum metallic blue-green; microlines on dorsal surface not visible at magnification of 50X, except labrum with meshes isodiametric; dorsal surface punctate, each puncture with long seta; elytral intervals each uniseriately punctate, each puncture extended about width of interval, except punctures of interval 1 smaller; frontal impressions of head, median longitudinal impression of pronotum, and scutellar interneur very deep; eyes small, temples tumid, large; pronotum markedly cordate, base sharply lobed, posterior angles acute; metasternum short, metepisternum quadrate; hind wings short stubs; elytra with humeri sharply ridged, projected forward; stylomere 2 of ovipositor with microsculpture very coarse (Figs. 116A-E), extended apically as ridges and spines. Standardized Body Length 3.80- 4.04 mm. (three specimens).

*Notes about relationships.*— Adults of this southeastern Australian species most closely resemble those of a probably undescribed species, known from a single female collected in southern West Australia (Margaret River; MCZ). The single male of *A. angusticollis* (Sloane) (Wiluna; MCZ) shares with the above species the coarse, generally punctate dorsum. However, it is much larger, and the basal lobe of the pronotum is less distinctly developed.

Subtribe DROMIINA

The exact composition of this subtribe has not been settled. Jeannel (1949: 990) chose to include in the subfamily Dromiitae (family Lebiidae) the dromiines (*sensu stricto*) and the demetriines, ranking these groups as tribes. He excluded *Apristus* Chaudoir, placing this genus in the family Lionychidae. Habu (1967) chose to rank demetriines and dromiines as subtribes of Lebiini, and to include the lionychid genera in the Dromiina. We elect to follow Habu, though we exclude *Celaenephes* Schmidt- Goebel.

Jeannel (1949: 915) also erected the tribe Singilini (subfamily Lebiinae) to include a number of genera whose adults are characterized by small size, and pale, hairy integument.

Mateu (1963) revised this complex, pointing out that three groups were included, which he ranked as tribes: Lichnasthenini, Singilini (*sensu stricto*), and Somotrichini. Ball (1975: 152) transferred the somotrichine to the subtribe Pericalina (*sensu lato*). It seems to us that lichnasthenines and singilines, as understood by Mateu, can best be accommodated in the Dromiina, and we place them here. For the present, the names Singilini and Lichnasthenini are treated as junior synonyms of Dromiina.

On the basis of shared similarities in details of ovipositor sclerites and form of median lobe, we add to the singiline assemblage of the Dromiina the following taxa that were included by Csiki (1932: 1497- 1498) in the subtribe Cymindina: *Metaxymorphus* Chaudoir, 1850; *Periphobus* Péringuey, 1896; and *Callidomorphus* Péringuey, 1896. Members of these taxa are so similar to one another that it is inappropriate to rank them as genera. Nonetheless, adults of each group are distinguished from one another on the basis of body form (see key, below). Consequently, we rank each as a subgenus of *Metaxymorphus*, the senior name.

Notes are also included about *Coptoptera*, for reasons given below.

### *Metaxymorphus* Chaudoir, *SENSU NOVO*.

Figs. 118A-B and 126A-B

*Metaxymorphus (sensu stricto)* Chaudoir, 1850: 370. GENERITYPE: *Dromius frenatus* Dejean, 1831: 351 (original designation). Péringuey, 1896: 205.—Csiki, 1932: 1497.—Basilewsky, 1958a: 295.—1961c: 216- 217.

*Periphobus* Péringuey, 1896: 204, 211. GENERITYPE: *P. ferox* Péringuey, 1896: 211 (monotypy).—Csiki, 1932: 1498.—Basilewsky, 1956: 236- 242.—1958a: 296. NEW SYNONYMY.

*Callidomorphus* Péringuey, 1896: 204, 210. GENERITYPE: *Metaxymorphus vittiger* Chaudoir, 1877: 234 (monotypy).—Csiki, 1932: 1498.

We are not in position to give diagnostic features of adults of this genus, for we do not know the other genera of dromiines well enough. We note, however, that the basis for assigning *Metaxymorphus* to the Dromiina is: head without suborbital setigerous punctures; elytron with penultimate umbilical setigerous puncture not laterad of antepenultimate and ultimate punctures; scutellar interneur separate from interneur 1, base of latter present; tibiae average, spinose; tarsomeres slender, glabrous dorsally, male front tarsomeres expanded slightly, with biseriate adhesive vestiture ventrally; tarsal claws pectinate; median lobe of males with basal bulb very small (Figs. 124A - 226A), right paramere very small (Fig. 125D); ovipositor with stylomeres 1 and 2 subequal, both glabrous, stylomere 2 with preapical "orifice" (membranous area, Figs. 121-123), preapical sensory furrow absent.

**Description.**— Smaller than average, Standardized Body Length ca. 3.2-4.5 mm. Form about average for Carabidae. Color somber: uniformly rufous to testaceous, or elytra striped alternately rufo-testaceous and testaceous; appendages paler than dorsum.

**Microsculpture.** Dorsum with meshes generally isodiametric to transverse on pronotum and elytra, microlines clearly visible at 50X. Venter and lateral sclerites of thorax with meshes transverse.

**Luster.** Dorsal surface dull; ventral surface faintly iridescent.

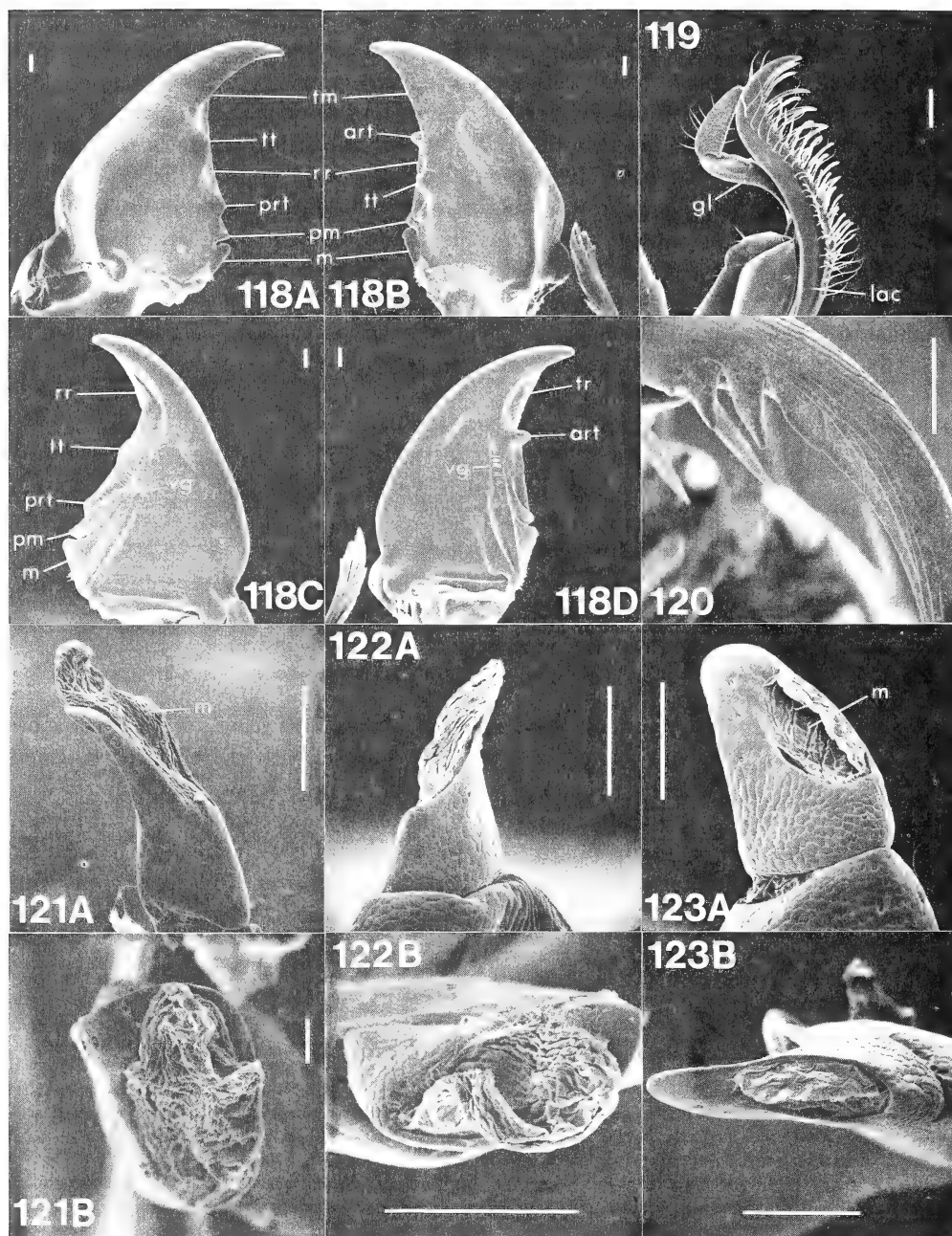
**Fixed setae.** Average for lebiines. Head with two pairs of supraorbital setigerous punctures; submentum and mentum each with single pair. Pronotum with two pairs of lateral setigerous punctures, posterior pair near posterior angles. Elytron with two discal setigerous punctures in interval 3; umbilical series continuous, of 13 or 14 setigerous punctures. Legs with average setation: tibiae with full complement of spines; tarsomere 5 with row of setae on each ventro-lateral margin. Abdominal sternum VII of both males and females with four setigerous punctures.

**Vestiture and surface.** Dorsal and ventral surfaces essentially glabrous, impunctate. Antennomere 1 with single seta; antennomeres 2 and 3 each with ring of setae preapically; remaining antennomeres average for lebiines.

**Head.** Average in form for lebiines, as broad or broader than average. Frontal impressions indistinct or well developed. Clypeus transverse, about rectangular, or with anterior margin distinctly incised, concave. Eyes average. Antenna filiform, antennomere 3 distinctly longer than 4; antennomeres each longer than wide.

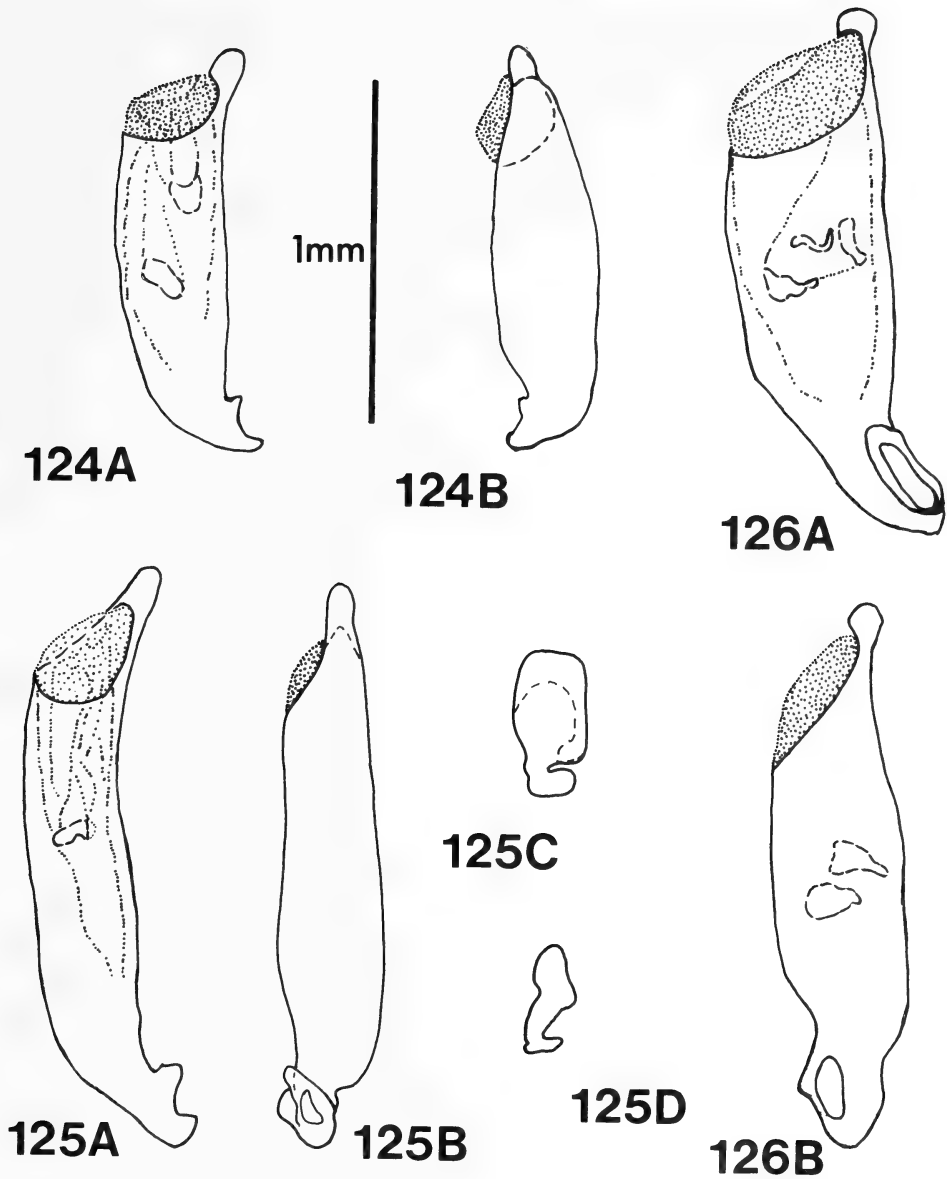
**Mouthparts.** Labrum transverse, about rectangular. Mandibles (Figs. 118A-D) trigonal, but overall asymmetric, left with anterior portion of terebra much narrower than anterior portion of right terebra (Figs. 118A and B). Left mandible





Figs. 118–123. SEM photographs of structures of Dromiina, genus *Metaxymorphus*.—Fig. 118: *M. (Periphobus) confusus* (Basilewsky), mandibles—A and C, left, dorsal and ventral aspects, respectively; B and D, right, dorsal and ventral aspects, respectively. Fig. 119: *M. (P.) confusus*, right maxilla, ventral aspect. Fig. 120: *M. (P.) confusus*, tarsal claw, terminal aspect. Figs. 121–123: Left stylomere 2. Fig. 121: *Metaxymorphus (sensu stricto)* species—A and B, lateral and ventral aspect, respectively. Fig. 122: *M. (P.) confusus*—A and B, medial and apico-ventral aspects, respectively. Fig. 123: *M. (Callidomorphus) vittiger* (Péringuey)—A and B, lateral and ventral aspects, respectively. Scale bars: 118A–D, and 119 = 100  $\mu$ m; 120–123B = 50  $\mu$ m. Legend, mandibles: art, anterior retinacular tooth; m, molar; pm, premolar; prt, posterior retinacular tooth; tm, terebral margin; tt, terebral tooth; vg, ventral groove. Legend stylomere 2: m, preapical membrane.





Figs. 124–126. Line drawings of structures of Dromiina, genus *Metaxymorphus*.—Male genitalia, A and B, median lobe, left lateral and ventral aspects, respectively; C and D, left and right parameres, respectively, ventral aspect. Fig. 124: *M. (sensu stricto)* species. Figs. 125: *M. (Periphobus) confusus* (Basilewsky). Fig. 126: *M. (Callidomorphus) vittiger* (Péringuey).

(Figs. 118A and C) with blunt, broad terebral tooth, terebral margin distinct for most of length of terebra; cutting edge retinacular ridge, anterior retinacular tooth small; posterior retinacular tooth prominent, with well developed ridge internally; molar tooth prominent, clearly isolated from premolar tooth; ventral groove (Fig. 118C) short, asetose. Right mandible (Figs. 118B and D) with cutting edge terebral margin anteriorly, retinacular ridge posteriorly; terebral tooth blunt, not as broad as that of left mandible; retinacular ridge prominent, anterior tooth conical, prominent, posterior tooth well developed, with well developed ventral ridge; ventral groove short, setae few. Maxilla average in form; lacinia with single row of setae on ventral surface (Fig. 119); galeomere 2 shorter than 1 coarsely sculptured; palpomeres slender, palpomere 4 appreciably longer than 3, fusiform, narrowed apically. Labium average, mentum with well developed tooth, and epilobes widened apically; glossal sclerite broad, apically with pair of long setae, and several shorter setae; paraglossae adnate to glossal sclerite, about as long as latter, each with row of rather large setae apically; palpomeres average in form, sparsely setose, palpomere 2 longer than 3, with two long setae; palpomere 3 fusiform, narrowly truncate at apex.

Thorax. Pronotum markedly to slightly transverse, constricted posteriorly; all margins sharply beaded; anterior margin slightly concave; posterior margin curved, but not lobate; sides rounded, incurved evenly posteriorly, not sinuate; disc slightly convex, lateral grooves narrow; median longitudinal impression well developed. Prosternum with apex of intercoxal process immarginate. Metathorax reduced, metepisternum either quadrate or wider than long (i.e., length of anterior margin greater than that of lateral margin).

Legs. Average for lebiines. Tibiae with well developed spines. Front tarsomeres 1- 3 of males slightly expanded, each with two rows of adhesive vestiture ventrally. Tarsomere 4 with apical margin truncate. Claws pectinate, pectinations small (Fig. 120) few (one-three per claw).

Elytra. Average for lebiine adults, though humeri more sloped than average; apical margin subtruncate to truncate. Interneurs shallow, impunctate; intervals flat to slightly convex; basal ridge sinuate, extended from humerus to edge of scutellum.

Wings. Short stubs.

Abdominal sterna II- VII average for lebiines.

Male genitalia. Median lobe (Figs. 124A, B - 126A, B) cylindrical, anopic; basal bulb markedly reduced; apical orifice on left side. Internal sac with various sclerites. Right paramere reduced (Fig. 125D).

Ovipositor and associated sclerites. Stylomeres 1 and 2 without ensiform or nematoid setae (Figs. 121-123), subequal. Stylomere 2 with part of ventral surface membranous, membrane seemingly exsertile; without preapical sensory furrow and associated sense organs of ventral surface.

### Key to Subgenera of *Metaxymorphus* (*sensu lato*)

- 1 (0) Clypeus sloped ventrally rather abruptly, depressed medially, or not. Head broad, body robust ..... *Periphobus* (*sensu lato*) Péringuey.
- 1' Clypeus sloped gradually anteriorly, surface plane, not depressed medially. Head narrower, body slender, agonoid ..... 2.
- 2 (1') Elytra bicolored, laterally testaceous, medially with more or less extensive, irregular, rufo-testaceous to piceous dark mark ..... Subgenus *Metaxymorphus* Chaudoir. p. 197
- 2' Elytra bicolored, pattern regular, margin and intervals 1, 3, 5, and 7 testaceous, intervals 2, 4, 6, and 8 rufo- piceous to piceous ..... Subgenus *Callidomorphus* Péringuey.

*Notes about classification.*— We explained above our reasons for including the species of *Metaxymorphus*, *Callidomorpha*, and *Periphobus* in a single genus.

Csiki (1932: 1497- 1498) listed the names of 19 valid species of *Metaxymorphus* (*sensu stricto*), to which Basilewsky (1961c: 216- 217) added *M. flaviceps* Motschulsky, and *M. discopennis* Motschulsky, having transferred them from *Charopterus*. Most of the species were described by Péringuey. According to Basilewsky (1958a: 295), it is impossible to interpret with certainty most of Péringuey's descriptions. It will be necessary, therefore, to revise this group, on the basis of a careful study of type material.

Basilewsky (1956: 236- 242) revised *Periphobus* Péringuey. Noting that the striking sexual dimorphism recorded by Péringuey was the result of combining material of two species under a single name, Basilewsky included the female co-type of *P. ferox* Péringuey (type locality-

Oudtshoorn) in the new species *P. confusus* Basilewsky. He provided illustrations of habitus (Fig. 1, *P. ferox*; Fig. 4, *P. confusus*) and of the male genitalia (Fig. 2a, *P. confusus*; Fig. 2b, *P. ferox*) for both species. (As noted on reprints, captions for Figs. 3 and 4 were reversed). The habitus illustration was reproduced as Fig. 39 in "South African Animal Life" (Basilewsky, 1958a: 296).

According to the description and key (Basilewsky, 1956: 238), heads of *P. ferox* specimens are more markedly modified than are heads of *P. confusus*. Furthermore, the heads are sexually dimorphic, especially those of *P. ferox*. However, this dimorphism is not as extreme as Péringuey believed.

*Notes about habitat.*— We did not locate information for *Metaxymorphus*. We surmise, however, on the basis of brachyptery, color, and form of adults, that they inhabit dry, open area, and live on the ground.

*Geographical distribution.*— This genus is known only from localities in the Union of South Africa.

*Specimens examined.*— We have seen 40 specimens of *Metaxymorphus* (*sensu lato*), from the following localities in South Africa.

*M. (Metaxymorphus) atriceps* Péringuey. Male, Cape Colony, Uitenhaage, Rv. J. O. Neil 1917- 55 (BMNH). Male, Cape Colony, Port Elizabeth G. A. K. Marshall 1917- 55 (BMNH).

*M. (M.) cursor* Péringuey. Male, female, Capetown, G. A. K. Marshall 1917- 55 (BMNH).

*M. (Metaxymorphus) species?*— 12 males, 15 females, all from Cape Province. IV. 1958 E. S. Ross, R. E. Leech (CAS). Male, two females, 19 mi. SE Garies 220 m V.2. 58; E. S. Ross, R. E. Leech (CAS). Four males, two females, 3 mi. SW Ladysmith 475 m. IV.24.58; E. S. Ross, R. E. Leech (CAS). Four males, female, Strandfontein XI.13.49 B. Malkin (CAS). Three males, nine females, Urendenburg XI.19.49 B. Malkin (CAS).

*M. (Callidomorphus) vittiger* Chaudoir. Male, Capland, Algoa Bay Dr. Brauns (BMNH). Female, Cape Colony Uiteahage Rev. J. O. Neil 1917- 55 (BMNH).

*M. (Periphobus) confusus* Basilewsky. Four males, Cape Province 5 mi. W. Herold 600 m. IV.24.58; E. S. Ross, R. E. Leech (CAS). Three females, Cape Province 3 mi. SW Ladysmith 475 m. IV.24.58; E. S. Ross, R. E. Leech (CAS).

### *Coptoptera* Chaudoir

*Coptoptera* Chaudoir, 1837: 5. GENERITYPE: *Coptoptera brunnea* Chaudoir, 1837: 5 (monotypy).-- Péringuey, 1896: 230 (in part).-- Basilewsky, 1956: 401.

*Klepsiphrus* Péringuey, 1896: 223, 237. GENERITYPE: *Klepsiphrus pugnax* Péringuey, 1896: 237 (monotypy).

*Syndetus* Péringuey, 1896: 204, 222. GENERITYPE: *Syndetus simplex* Péringuey, 1896: 222 (monotypy).--Basilewsky, 1958b: 340-341.

*Notes.*— The genus *Syndetus* was included in the Cymindina by Péringuey (1896: 223), though he pointed out that specimens of *S. simplex* had dromiine features, as well. Basilewsky, who examined the type of *S. simplex*, subsequent to his revision of *Coptoptera* (1956), concluded that this species was not only a dromiine, but also that it was a species of *Coptoptera*. We have not seen specimens of this species, but we accept Basilewsky's judgement.

### Tribe ZUPHIINI

The genus *Agastus* Schmidt-Goebel was included by Jedlička (1963: 451) in the Cymindina, but this genus clearly belongs in the Zuphiini-- where Csiki (1932: 1567) placed it. The senior author saw in the British Museum (Natural History) a specimen of *A. ustulatus* Gestro from Java, and another with an indecipherable locality label, that was compared with the type.

## CONCLUDING REMARKS

This paper began with the seemingly limited objective of seeking for the sister group of a New World taxon of lebiines. It developed into a taxonomic treatment, based on barely adequate material of groups ranging in rank from intra-specific to subtribal. Because so much of the work centered around dismembering of a taxon treated previously as if it were a taxonomically valid entity, and because of a shortage of time as well as of material for study, the paper was frustrating to write. Taxonomists, like most other scientists, prefer to build, rather than to take apart. Building for taxonomists consists primarily of description of new taxa, and locating such in the system of previously described taxa. Nonetheless, re-organization of groups like the cymindines of authors is required if future workers are to have a more secure basis for proceeding with classification of the Lebiini.

We reiterate our belief that future progress will be along lines that Habu pioneered. We wish to present briefly our views about how research on lebiines should proceed to produce maximally useful results in minimum time. It seems to us that development of a general system of classification for the Lebiini could be obtained in two stages. The first is undertaking of regional studies, zoogeographical region by region. Publications could consist of broad-spectrum reviews, based on dissections of representative members of each of the described genera, in order to test further those characters that seem to be important, and to assign these taxa to proper subtribes. At the same time, keys to genera ought to be written, and species names catalogued.

Stage 2 would have a taxonomic focus, with all of the genera of the world of each subtribe being assembled on the basis of inferred phylogenetic relationships. Persons doing this work would have the data base assembled by regional studies to guide them. Additionally, inter-regional comparisons would likely unearth additional character systems for use in classification. At this stage, the search for sister groups both within and between tribes would be of substantial importance and might lead to re-defining the limits of the Lebiini, either by exclusion of some subtribes, or by inclusion of other lebiomorph tribes.

Because much taxonomic research is on a regional basis, we believe that the initial regional approach advocated here to re-classification of lebiine genera will lead quickly to publications that are of immediate interest and use. Such publications are likely to provide the impetus for accumulation of additional data that will be of use in the world-wide treatment of genera of individual subtribes.

A second general issue about which comments seem appropriate is ranking of taxa. So long as one works within a geographically limited fauna, one can adopt the generic concepts that have been applied by previous workers in that area. However, a study of a group on a world-wide basis requires adoption of a uniform treatment. In this study, we were required to deal with the discrepancy between a broad concept of genera advocated by Lindroth (1969b: XVII) as applied to Holarctic carabids, and the more restricted one advocated explicitly by Basilewsky (1968b: 185) in his studies of African taxa, and applied by Mateu in his studies of tropical lebiines, generally. We believe that more broadly defined genera are more useful to biologists other than taxonomists, and that units more difficult to recognize and more restricted geographically can be named, but ranked at a lower level. Thus, we have defined genera broadly, in spite of the discomfort that will be caused to some of our colleagues.

Procedure in ranking is not a matter of right and wrong, but one of taste and preference--unless one adheres strictly to the tenets of cladistics. We hope that our re-ranking of

well-known taxa will be judged on the merits advocated, and will be found satisfactory for general use. We hope that our judgements will not be rejected out of hand.

Reference above to biologists other than taxonomists recalls the interrelationships between these two groups, specifically with reference to the Lebiini. So far, study of lebiines has been principally the playground of taxonomists. In the course of their studies, such workers have discovered clues suggestive of modes of life and behavior that ought to excite interest of ecologists and ethologists, as well as of economic entomologists. When such workers take up the challenges inherent in determining life histories, host-parasite relationships, other ecological relationships, and behavior patterns, the data produced will be of great value to taxonomists, and will no doubt help in resolving vexing taxonomic problems.

Finally, we return to the initial purpose of this paper: a search for a sister group, specifically that of *Pinacodera* Schaum. We think that we have found it, though we are not sure. At least we have shed some light on the problem, and will develop hypotheses on the basis of our work. Hennig (1966: 139) noted that an important task of phylogenetic systematics is search for sister groups of monophyletic taxa. By accepting his formulation of tasks of systematics, we have been able to examine a range of interesting problems. As others have stated, Hennig's methods seem fruitful. They should be used widely to seek understanding of important practical taxonomic problems, rather than to serve as the basis for the futile and arid debate that rages in current issues of "Systematic Zoology" and elsewhere, the tone of which is reminiscent of the writings of Medieval scholastics addressing theological problems that seem now of little consequence.

#### ACKNOWLEDGEMENTS

For the loan of material on which this study is based, we thank the following curators: M. E. Bacchus and P. M. Hammond (BMNH); D. H. Kavanaugh (CAS); B. P. Moore (CSIRO); G. Demoulin (IRSB); P. Basilewsky (MACT); R. J. McGinley and A. E. Newton (MCZ); J.-J. Menier and H. Perrin (MNHP); V. Whitehead (SAMC); T. L. Erwin (USNM); and T. Sen Gupta (ZSIC). Peter A. Meyer, Heidelberg, Victoria, Australia, presented to the Strickland Museum various Australian lebiines that were very important to this study, and also provided some of the inspiration for its undertaking.

For courtesies extended during visits to their respective institutions, the senior author is grateful to: M. E. Bacchus and P. M. Hammond; P. Basilewsky; G. Demoulin; T. L. Erwin; D. H. Kavanaugh; and R. J. McGinley and A. E. Newton.

James Liebherr (Department of Entomology, University of California, Berkeley, California) made available to us a manuscript about affinities of lachnophorines that caused us to alter our original view about this topic.

A preliminary draft of the typescript was reviewed by Terry L. Erwin, Ronald B. Madge (CIE- BMNH), and Barry P. Moore, who made valuable suggestions for improving the substance of the text, and who located numerous minor errors of omission and commission.

We received substantial assistance with preparation of illustrations from members of the technical staff of our Department. We note especially contributions of D. Shpeley and G. B. Braybrook, in preparing specimens and taking photographs with the Scanning Electron Microscope. We also thank J. S. Scott for his meticulous attention to detail in preparing the plates for publication. Various versions of the manuscript were typed by I. E. Bergum, and C. Shirt, and we appreciate very much the care taken and the interest shown in producing the final

manuscript.

We also acknowledge assistance of J. E. O'Hara, who undertook a search of the literature for current publications about cymindines.

#### NOTE ADDED IN PROOF

After this paper was nearly ready for publication, R. B. Madge (*in litt.*) advised us that Habu (1982:113) had erected the *Celaenephina* as a new subtribe for *Celaenephes* Schmidt-Goebel, though he expressed doubt (*loc. cit.*: 110) that this genus belonged in the Lebiini. He also diagrammed (*loc. cit.*: 114, Fig. 29) his views about evolution of the stylomeres of truncatipennian carabids, with those of *Celaenephes* either in an ancestral position, or outside this taxonomic complex. Thus, our views, expressed above, are basically in agreement with those of Habu.

#### REFERENCES

- Allen, R.T. and G.E. Ball. 1980. Synopsis of Mexican taxa of the *Loxandrus* series (Coleoptera: Carabidae: Pterostichini). Transactions of the American Entomological Society 105: 481–576.
- Alluaud, C. 1917. Les carabiques de la faune alpine des hautes montagnes de l'Afrique orientale. Annales de la Société entomologique de France 86: 73–116.
- Andrewes, H.E. 1923. Papers on Oriental Carabidae XII. Annals and Magazine of Natural History (9) 12: 679–690.
- \_\_\_\_\_. 1929. Coleoptera Carabidae. Volume 1.—In Stephenson, J. (Editor). The fauna of British India, including Ceylon and Burma. Taylor and Francis, London. xviii + 431 pp., 5 plates.
- \_\_\_\_\_. 1930. Catalogue of Indian Insects. Part 18—Carabidae. Calcutta. 389 pp.
- \_\_\_\_\_. 1935. Keys to some Indian genera of Carabidae. V. The genera *Cymindoidea*, *Platytarus*, and *Taridius*. Stylops 4: 201–205.
- Antoine, M. (1938) 1939. Notes d'entomologie marocaine. XXIX. Bulletin de la Société des Sciences naturelles et physiques du Maroc 18: 170–191.
- \_\_\_\_\_. 1962. Coléoptères carabiques du Maroc. Cinquième partie. Mémoires de la Société des Sciences naturelles et physiques du Maroc, Zoologie, Nouvelle Serie No. 9: 539–692.
- Ball, G.E. 1960. Carabidae, Fascicle 4, pp. 55–210. In Arnett, R.H. 1960. The beetles of the United States (a manual for identification). The Catholic University of America Press, Washington, D. C. xi + 1112 pp.
- \_\_\_\_\_. 1975. Pericaline Lebiini: notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). Quaestiones Entomologicae 11 (2): 143–242.
- \_\_\_\_\_. 1978. The species of the Neotropical genus *Trichopselaphus* Chaudoir (Coleoptera: Carabidae: Harpalini): classification, phylogeny and zoogeography. *Ibid.* 14 (4): 447–489.
- \_\_\_\_\_. 1982. Evaluation of the Baron Maximilien de Chaudoir's contribution to classification of cymindine Lebiini and Masoreimorphi. The Coleopterists Bulletin 36

(3): 512–529.

- \_\_\_\_\_ and D. Shpeley. In press. The species of eucheiloid Pericalina: classification and evolutionary considerations. *The Canadian Entomologist*.
- Basilewsky, P. 1953a. Carabidae (Coleoptera Adephaga). Exploration du Parc national de l'Upemba. Mission G. F. de Witte, *et alii*. (1946–1949). Fascicule 10. Institute des Parcs nationaux du Congo Belge. Bruxelles. pp. 1–252.
- \_\_\_\_\_. 1953b. Contributions à l'étude des Coléoptères carabiques de la région malgache. *Mémoires de l'Institut scientifique de Madagascar Serie III*: 53–65.
- \_\_\_\_\_. 1954a. Le genre *Leptosarcus* Péringuey (Coléoptère Carabidae Lebiinae). *Bulletin de la Société entomologique de Belgique* 90: 83–88.
- \_\_\_\_\_. 1954b. Revision des genres *Hystrichopus* Boheman et *Plagiopyga* Boheman (Coleoptera: Carabidae Lebiinae). *Annales du Musée Royal du Congo Belge, Tervuren (Série 8°) Science Zoologie* 31: 7–99.
- \_\_\_\_\_. 1954c. Le genre *Pseudomasoreus* Desbrochers. *Revue Zoologique et Botanique d'Afrique* 49 (1–2): 89–96.
- \_\_\_\_\_. 1956. Contributions à la connaissance des Lebiinae d'Afrique (Coleoptera Carabidae) II. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 92: 236–248.
- \_\_\_\_\_. 1957. Contributions à la connaissance des Lebiinae d'Afrique III. (Dromiinae: *Klepterus* Péringuey et *Klepteronimus* Péringuey). *Ibid.* 93: 239–256.
- \_\_\_\_\_. 1958a. Coleoptera Carabidae, 5: 212–317. In Hånstrom B., P. Brinck, and G. Rudebeck. 1955–1973. *South African Animal Life, Results of the Lund University Expedition in 1950–1951. Volumes 1–15.* Almqvist and Wiskells Boktryckeri AB.
- \_\_\_\_\_. 1958b. Contributions à la connaissance des Lebiinae d'Afrique. IV. (Coleoptera Carabidae). *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 94: 323–341.
- \_\_\_\_\_. 1960. Coléoptères Carabidae du Mont Kabobo recueillis par N. Leleup. *Revue Zoologique et Botanique d'Afrique* 62: 66–90.
- \_\_\_\_\_. 1961a. Contribution à la connaissance des Lebiinae d'Afrique (Coleoptera: Carabidae) VII. *Ibid.* 64: 153–171.
- \_\_\_\_\_. 1961b. Coléoptères Carabidae africains nouveaux XII. *Ibid.* 63: 113–127.
- \_\_\_\_\_. 1961c. Sur les types de Carabidae africains décrits par V. Motschulsky. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 97: 205–224.
- \_\_\_\_\_. 1962. LX. Coleoptera Carabidae. Mission zoologique de l'I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup, 1957). *Annales du Musée Royal d'Afrique Centrale (Ser. 8°) Science Zoologie* No. 107: 46–337.
- \_\_\_\_\_. 1968a. Missione 1965 del Prof. Giuseppe Scortecchi nello Yemen (Arabie meridionale). *Atti della Societa Italiana di Scienze Naturale di Milano*. 107 (III–IV): 349–361.
- \_\_\_\_\_. 1968b. III. Les calosomes des îles Galapagos (Coleoptera Carabidae). In *Mission zoologique belge aux îles Galapagos et en Ecuador* (N. et J. Leleup, 1964–1965). Vol. I, pp. 179–207. L'Imprimerie des Sciences, s. a., Bruxelles.
- \_\_\_\_\_. 1976. 19. Coleoptera Carabidae. Mission entomologique du Musée

- Royal d l'Afrique Centrale aux Monts. Uluguru, Tanzanie (L. Berger, N. Leleup, et J. Debecker, V–VIII. 1971). *Revue de Zoologie Africaine* 90 (3): 671–721.
- \_\_\_\_\_. 1982. Contributions a l'etude des Coléoptères carabiques de la region malgache XIV. Description d'un genre nouveau de Madagascar. *Bulletin de la Société entomologique de France* 87: 20–24.
- Bates, H.W. 1871. Notes on Carabidae, and descriptions of new species (No. 7). *Entomologists' Monthly Magazine* 8: 77–81.
- \_\_\_\_\_. 1872. Notes on Carabidae, and descriptions of new species (No. 12). *Ibid.* 8: 199–202.
- \_\_\_\_\_. 1878. New genera and species of Carabidae from Tasmania. *Cistula Entomologica* II: 317–326.
- \_\_\_\_\_. 1883. Insecta, Coleoptera, Carabidae, Cicindelidae, supplement, Vol. 1, part 1, pp. 153–256, plates vi–vii. In Godman, F.D. and O. Salvin. 1879–1911. *Biologia—Centrali Americana. Coleoptera*. 7 volumes in 17 parts. London.
- \_\_\_\_\_. 1884. *Ibid.* pp. 257–299, plate xiii. *Ibid.*
- \_\_\_\_\_. 1886. On the geoadephagous Coleoptera collected by Mr. George Lewis in Ceylon. *Annals and Magazine of Natural History (series 5)* 17: 68–81, 143–156, and 199–212.
- \_\_\_\_\_. 1892. List of the Carabidae. *Viaggio di Leonardo Fea in Birmania e regioni vicine. Annali del Museo Civico di Storia Naturale di Genova Series 2a* 12 (32): 267–428.
- Bedel, L. 1906. Catalogue raisonné des coléoptères du nord de l'Afrique (Maroc, Algérie, Tunisie, et Tripolitaine) avec notes sur la faune des Isles Canarie et de Madère. pp. 201–264. Paris.
- Blackburn, T. 1894. Further notes on Australian Coleoptera, with descriptions of new genera and species. Parts XV–XVI. *Transactions of the Royal Society of South Australia* 18: 139–168; 200–240.
- \_\_\_\_\_. 1901. Further notes on Australian Coleoptera, with descriptions of new genera and species. Parts XXVIII–XXIX. *Transactions and Proceedings of the Royal Society of South Australia* 25: 99–131.
- \_\_\_\_\_. 1908. Further notes on Australian Coleoptera, with descriptions of new genera and species. No. XXXVIII. *Transactions of the Royal Society of South Australia* 32: 362–386.
- Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part I. *Bulletin of the United States National Museum* No. 185, pp. 1–188.
- Blanchard, C.E. 1853. Description des insectes. Voyage au Pole Sud ..... *Zoologie* vol. 4. Paris. 422 pp.
- Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. The Nature Publishing Company, Indianapolis, Indiana. 1386 pp.
- Boheman, C.H. 1848. *Insecta Caffraria annis 1838–1845a J.A. Wahlberg collecta. Coleoptera*, Vol. 1, part 1. Fritze und Nordstedt, Holmiae. 298 pp.
- Burgeon, L. 1937. Catalogues raisonnés de la faune entomologique du Conge Belge. Coléoptères carabiques (Troisième Partie). *Annales de Musée du Congo Belge*.



Zoologie Série III Section II, Tome II, Fascicule 5: 315-406.

Casey, T.L. 1920. Random studies among the American Caraboidea. *In* Casey, T.L. *Memoirs on the Coleoptera*, Volume IX, pp. 133-299. New Era Publishing Company, Lancaster, Pennsylvania. 516 pp.

Castelnau (Comte de), F.L.N. de C. Laporte 1832. Mémoire sur cinquante espèces nouvelles ou peu connues d'insectes. *Annales de la Société entomologique de France* 1: 386-415, 448.

Chaudoir, M. de. 1837. Description de quelques genres nouveaux et de quelques espèces nouvelles ou inédites de carabiques. *Bulletin de la Société des Naturalistes de Moscou* 10 (3): 3-20.

\_\_\_\_\_. 1850. Mémoire sur la famille des carabiques (2e partie, cont.). *Ibid.* 23: 349-460.

\_\_\_\_\_. 1852. Memoire sur la famille des carabiques, Part 3. *Ibid.* 25: 3-104.

\_\_\_\_\_. 1871. Remarques sur le catalogue de MM. de Harold et Gemminger, Tome 1. *Ibid.* 44 (II): 279-287.

\_\_\_\_\_. 1873. Essai monographique sur le genre *Cymindis* proprement dit. *Berliner Entomologischer Zeitschrift* 17: 53-120.

\_\_\_\_\_. 1875. Genres aberrants du groups des cymindides. *Bulletin de la Société Impériale des Naturalistes de Moscou* 49 (II): 1-61.

\_\_\_\_\_. 1877. Genres nouveaux et espèces inédites de la famille des carabiques. *Ibid.* 51: 188-268.

\_\_\_\_\_. 1878. Révision des genres *Onychopterygia*, *Dicranoncus*, et *Colpodes*. *Annales de la Société entomologique de France* (5) 8: 275-382.

Csiki, E. 1932. Coleoptera, Carabidae, Pars. 124, Harpalinae VII, pp. 1279-1598. *In* Junk W. und S. Schenkling. 1909-Coleopterorum Catalogus. W. Junk, Berlin und 's-Gravenhage.

Darlington, P.J., Jr. 1952. The carabid beetle of New Guinea. Part 2. The Agonini. *Bulletin of the Museum of Comparative Zoology* 107 (3): 89-252, 4 plates.

\_\_\_\_\_. 1968. *Ibid.* Part III. Harpalinae (continued): Perigonini to Pseudomorphini. *Ibid.* 137(1): 1-253.

\_\_\_\_\_. 1971. *Ibid.* Part IV General considerations; analyses and history of fauna; taxonomic supplement. *Ibid.* 142 (2): 130-337.

Dejean, P.F.M.A. 1825. Spécies général des coléoptères de la collection de M. le comte Dejean. Vol. 1. Méquignon-Marvis, Paris. xxx + 463 pp.

\_\_\_\_\_. 1826. *Ibid.* Vol. 2. *Ibid.* viii + 501 pp.

\_\_\_\_\_. 1831. *Ibid.* Vol. 5. *Ibid.* viii + 883 pp.

Desbrochers des Loges, J. 1904. Faunule des Coléoptères de la France et de la Corse. Carabides de la Tribu des Lebiinae et des Tribus voisines. *Le Frelon*, 1904, No. 9, pp. 133-144; Nos. 10 and 11, pp. 145-176; and No. 12, pp. 177-196.

Dilger, W.C. 1952. The Brij hypothesis as an explanation for the tropical faunal similarities between the Western Ghats and the eastern Himalayas, Assam, Burma and Malaya. *Evolution* 6 (1): 125-127.

Emden, F.I. van. 1937. Neue und bekannte Carabidae aus Java (Coleoptera). *Arbeiten über morphologische und taxonomische Entomologie* 4 (2): 111-125.

Emetz, V.M. 1972. A revision of the ground beetles of the genus *Cymindis* Latr. (Coleoptera,

- Carabidae) of the fauna of the USSR. 1. The subgenera *Mastus* Motsch. and *Pseudomastus* Emetz, subgen. n. Entomological Reviews 51: 194–202 (translated from Russian).
- \_\_\_\_\_. 1973. Materials for the revision of the genus *Cymindis* Latr. (Coleoptera, Carabidae) of the fauna of the USSR. 2. Subgenera *Iscariotes* Reiche and *Neopsammoxenus* Emetz, subgen. n. *Ibid.* 52 (1): 102–107. (translated from Russian)
- Erichson, W.F. 1842. Beitrag zur Fauna von Vandiemensland, mit besonderer Rucksicht auf die geographische Verbreitung der Insekten. Archiv für Naturgeschichte, Vol. 8, Part 2: 83–287.
- Erwin, T.L. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: a revision of the New World–Australian genus *Pericompso* LeConte. Smithsonian Contributions to Zoology No. 162. Washington, D.C. iv + 96 pp.
- \_\_\_\_\_. 1978. Systematic, natural history, and zoogeographic notes on the genus *Agra* Fabricius, with a description of a new species from Panama (Coleoptera: Carabidae: Lebiini). The Coleopterists Bulletin 32 (4): 261–268.
- \_\_\_\_\_. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions (Coleoptera: Carabidae), pp. 539–592. In Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern (Editors). Carabid beetles: their evolution, natural history, and classification (Proceedings of the First International Symposium of Carabidology, Smithsonian Institution, Washington, D. C., August 21, 23, and 25, 1976). W. Junk b.v., publishers, The Hague. X + 644pp.
- \_\_\_\_\_. 1982. *Agra*, arboreal beetles of Neotropical forests: *erythropus* group systematics. Systematic Entomology 7 (1): 39–71.
- \_\_\_\_\_ and L.J.M. Erwin. 1976. Relationships of predaceous beetles to tropical forest wood decay. The natural history of Neotropical *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) and its implications in the evolution of ectoparasitoidism. Biotropica 8 (4): 215–224.
- \_\_\_\_\_, D.R. Whitehead, and G.E. Ball. 1977. Family 4. Carabidae, The Ground Beetles, pp. 4.1–4.68. In Blackwelder, R.E. and R.H. Arnett. Checklist of the beetles of Canada, United States, Mexico, Central America, and the West Indies. World Digest Publications, Oxytocis Pond, Wallase Road, Kinderhook, New York 12106.
- Fairmaire, L. 1850. *Platytarus*, nouveau genre de Coléoptères, établi pour *Cymindis* Fomini. Bulletin de la Société entomologique de France (2) 8: 17
- \_\_\_\_\_. 1901. Matériaux pour la faune coleopterique de la région Malgache (11e note). Revue d'Entomologie 20: 101–248.
- \_\_\_\_\_ and J.J.A. Laboulbène. 1854. Faune entomologique française ou description des insectes qui se trouvent en France, coléoptères, Vol. 1. Deyrolle, Paris. 180 pp.
- Fauvel, A. 1881. Communications. Annales de la Société entomologique de France. (6) 1: CXVIII.
- Fourcroy, A.F. de. 1785. Entomologia Parisensis, sive catalogus insectorum, quae in agro parisiensi reperiuntur. 2 vols. Paris. 544 pp.
- Gemminger, M. and E. von Harold. 1868. Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. I Cicindelidae–Carabidae. Paris, E. Deyrolle fils,

- 19 Rue de la Monnaie. XXXVI + 424 pp., index.
- Habu, A. 1967. Fauna Japonica. Carabidae, Truncatipennes Group (Insecta: Coleoptera). Tokyo Electrical Engineering College Press, Hakushin-Sha Printing Co., Tokyo, Japan. xiv + 338 pp. Plates I–XXVII, some in color.
- . 1978. Fauna Japonica Carabidae: Platynini. Yugaku-Sha Ltd., Tokyo, Japan. viii + 447 pp. Plates I–XXXVI, some in color.
- . 1982. Revised and supplementary notes on, and descriptions of the Truncatipennes group of Japan (Coleoptera, Carabidae). The Entomological Review of Japan 36 (2): 85–142.
- Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Chicago, London. Preface, Contents and 263 pp.
- Horn, G.H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Transactions of the American Entomological Society 9: 91–196, plates 1–10.
- . 1882. Synopsis of the tribe Lebiini. *Ibid.* 10: 126–164.
- Iakobson, G.G. 1907. Die Käfer Russlands und Westeuropas. Ein Handbuch zum Bestimmen der Käfer. Lieferung V.A.F. Devrient, St. Petersburg. pp. 321–400, plates 37–46 (in Russian).
- Jeannel, R. 1941. Sur le genre *Pseudomasoreus* Desbrochers. Bulletin de la Société entomologique de France 1941. pp. 62–67.
- . 1942a. Coléoptères carabiques, 2me partie. Faune de France 40: 573–1173. Paris
- . 1942b. La genese des faunes terrestres. Presses Universitaires de France, Paris. viii + 513 pp., 8 plates.
- . 1949. Coléoptères carabiques de la Region malgache (troisieme partie). Faune de l'Empire francais XI, pp. 767–1146, figs. 365–548.
- . 1955. L'édéage. Initiation aux recherches sur la systematique des Coléoptères. Publications du Muséum National d'Histoire Naturelle, Editions du Museum, 36, Rue Geoffroy-Saint-Hilaire (Ve) Paris. 155 pp.
- Jedlička, A. 1963. Monographie der Truncatipennen aus Ostasien Lebiinae–Odacanthinae–Brachyninae. Entomologische Abhandlungen und Berichte aus dem Staatl. Museum für Tierkunde in Dresden, 28 (7): 269–579, 244 text-figs., 54 plates, 6 colored.
- . 1968. Neue Carabiden aus der Palaearktischen Region (Coleoptera, Carabidae). Reichenbachia 8 (34): 285–296.
- Kolbe, H. J. 1898. Coleopteren (Kafer und Netzflugler). Deutsch-Ost-Afrika IV. Lief. VI, VII, VIII. Coleoptera 364 pp., 3 plates. Neuroptera, 42 pp., 1 plate (from Zoological Record, 1897, vol. 34: 34).
- Lacordaire, T. 1854. Histoire naturelle des Insectes, genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Vol. 1. Cicindeletes–Palpicornes. Libraire encyclopedique de Roret, Paris. x + 486pp.
- Larson, D.J. 1969. A revision of the genera *Philophuga* Motschoulsky and *Tecnophilus* Chaudoir, with notes on the North American Callidina (Coleoptera: Carabidae). Quaestiones Entomologicae 5 (1): 15–84.
- Latreille, P.A. 1806. Genera crustaceorum et insectorum secundem ordinem naturalem in

- familias disposita, iconibus exemplisque plurimus explicata. Vol. 1. Paris. XVIII + 303 pp.
- Lea, H.M. 1912. The late Rev. Canon Thomas Blackburn, B.A., and his entomological work. Transactions of the Royal Society of South Australia 36: v–xl.
- LeConte, J.L. 1851. Descriptions of new species of Coleoptera from California. Annals of the Lycaenum of Natural History of New York 5: 125–184.
- \_\_\_\_\_. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society (2) 10: 363–403.
- \_\_\_\_\_. 1861. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections III (No. 136): 1–286. Part 1.
- \_\_\_\_\_ and G.H. Horn. 1883. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. *Ibid.* 26 (4) (No. 507): xxxvii + 567 pp.
- Leng, C.W. 1920. Catalogue of the Coleoptera of America north of Mexico. John D. Sherman, Jr., Mount Vernon, New York. 470 pp.
- \_\_\_\_\_ and A.J. Mutchler, 1927. Supplement 1919–1924 (inclusive) to Catalogue of the Coleoptera of America north of Mexico. John D. Sherman, Mount Vernon, New York. 78 pp.
- Liebherr, J. MS. Larval description of *Calybe (Ega) sallei* (Chevrolat) with a preliminary assessment of anchonoderine affinities (Carabidae: Anchonoderini).
- Liebke, M. 1938. Denkschrift über die Carabiden-tribus Colliurini. Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand. Vol. 4, pp. 37–41. Riga.
- \_\_\_\_\_. 1951. Beiträge zur Fauna Perus. nach der Ausbeute der Hamburger Sudperu-Expedition 1936 ander Sammlungen wie auch auf Grund von Literaturangaben von Prof. Erich Titschack. Band II. Wissenschaftliche Bearbeitungen. Verlag Gustav Fischer, Jena. 344 pp.
- Lindroth, C.H. 1969a. The ground beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. Part 6. Opuscula Entomologica, Supplementum 34: 945–1192.
- \_\_\_\_\_. 1969b. *Ibid.* Part 1. *Ibid.* Supplementum 35: I–XLVIII.
- MacLeay, W.J. 1863–1866 (1864). Descriptions of new genera and species of Coleoptera from Port Denison. Transactions of the Entomological Society of New South Wales 1: 106–130, pl. IX.
- \_\_\_\_\_. 1871. Notes on a collection of insects from Gayndah. *Ibid.* 2: 79–158.
- Mahar, J.M. 1978. The life history of *Pinacodera limbata* Dejean and *Pinacodera platicollis* Say (Coleoptera: Carabidae) in oak forests in Michigan. Unpublished M.S. Thesis, Michigan State University, East Lansing, Michigan. 47 pp.
- Mandl, K. 1973. Bausteine zur Kenntnis der Familie Carabidae (Col.). Entomologischen Arbeiten aus den Museum Georg Frey 24: 88–100.
- Mannerheim, C.G. 1837. Mémoire sur quelques genres et espèces de carabiques. Bulletin de la Société Impériale des Naturalistes de Moscou 10 (2): 3–49.
- Mateu Sanpere, J. 1952. El género *Trymosternus* Chaudoir. Eos 28: 109–141.
- \_\_\_\_\_. 1958. Más datos sobre los *Trymosternus* Chaud. (Col., Carabidae) de la Peninsula Ibérica. Miscelánea Zoológica 1 (5): 1–6.
- \_\_\_\_\_. 1963. Notas sobre tres series filéticas de Lebiidae (Lichnasthenini Thomson, Singilini Jeannel, Somotrichini nov.) (Coleoptera-carabides) y rectificaciones sinonimicas. Annali del Museo Civico di Storia Naturali di Genova

74: 122–139.

- 
- \_\_\_\_\_. 1970a. Notes sur Lebiens malgaches (Coleoptera Carabidae) (premiere note). *Revue Zoologique et Botanique d'Afrique* 81 (1–2): 173–179.
- 
- \_\_\_\_\_. 1970b. Description d'un genre nouveau de Coléoptères Carabidae Lebiinae, representant d'une tribu inédite en Afrique. *Ibid.* 82 (1–2): 148–156.
- 
- \_\_\_\_\_. 1972. Remarques sur trois genres de Troncatipennes afro-asiatiques (Coléoptères Carabiques). *Nouvelle Revue d'Entomologie* 2: 43–52.
- 
- \_\_\_\_\_. 1974. Révision des espèces africaines et malgaches du genre *Euplynes* Schmidt-Goebel (Col. Carabidae Agonini). *Revue Zoologique Africains* 88 (3): 487–506.
- 
- \_\_\_\_\_. 1980. Notes sur les lébiens malgaches (5e note). Sur trois nouveaux *Pseudomasoreus* Desbrochers. *Revue francais d'Entomologie* (N. S.) 2 (1): 15–23.
- Matthews, E.G. 1980. A guide to the genera of beetles of South Australia. Part 1. Archostemata and Adephaga. Special Educational Bulletin Series South Australian Museum Adelaide, Australia. 48 pp., figs. 3–108.
- Moore, B.P. 1963. New or little-known Australian Carabidae in the Frey Museum (Col.). *Entomologischen Arbeiten aus den Museum Georg Frey* 14: 435–444.
- 
- \_\_\_\_\_. 1964. New cavernicolous Carabidae (Coleoptera) from mainland Australia. *Journal of the Entomological Society of Queensland* 3: 69–74.
- 
- \_\_\_\_\_. 1967a. New Australian cave Carabidae (Coleoptera). *Proceedings of the Linnaean Society of New South Wales* 91: 179–184.
- 
- \_\_\_\_\_. 1967b. New or little-known Australian Carabidae in the Frey Museum (Col.). *Entomologischen Arbeiten aus den Museum Georg Frey* 18: 308–322.
- Motschulsky, V. von. 1864. Enumération des nouvelles espèces de Coléoptères rapportés de ses voyages. *Bulletin de la Société Impériale des Naturalistes de Moscou* 337 (2): 171–240, 297–355.
- Noonan, G.R. 1973. The anisodctylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution, and zoogeography. *Quaestiones Entomologicae* 9 (4): 266–480.
- Péringuey, L. 1892. Fourth contribution to the South African Coleopterous Fauna. Descriptions of new species in the South African Museum. *Transactions of the South African Philosophical Society* 6 (2): 95–134.
- 
- \_\_\_\_\_. 1896. A descriptive catalogue of the Coleoptera of South Africa, part II. *Ibid* 7: i–xiv and 99–623, plates 3–10.
- Porta, A. 1923. *Fauna Coleopterorum Italica*. Volume 1. Adephaga. Piacenza, San Remo. 285 pp., 278 figs.
- Reichardt, H. 1974. The systematic position of *Asklepia* Liebknecht, 1938, with the description of a new species (Coleoptera, Carabidae). *The Coleopterists Bulletin* 28 (4): 177–179.
- 
- \_\_\_\_\_. 1977. A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). *Quaestiones Entomologicae* 13 (4): 347–485.
- Say, T. 1823. Descriptions of insects of the families Carabici and Hydrocanthari of Latreille inhabiting United States. *Transactions of the American Philosophical Society* (new series) 2: 1–109.
- Schaum, H. 1856–1860. *Naturgeschichte der Insecten Deutschlands*. Erste Abtheilung Coleoptera Erster Band. Nicolaische Verlagsbuchhandlung (G. Parthey), Berlin. 791

pp.

- Schmidt-Goebel, H.M. 1846. *Faunula Coleopterorum Birmaniae, adjectis nonnullis Bengaliae indigenis*. Lieferung 1. Prague. 94 pp., plates 1-3.
- Seidlitz, G. von. 1887-1891. *Fauna Baltica. Die Käfer (Coleoptera) der deutschen Ustseeprovinzen Russlands*. Königsberg. CXCII + 818 pp.
- \_\_\_\_\_. 1888-1891. *Fauna Transsylvanica. Die Käfer Siebenburgens*. Königsberg. LVI + 915 pp., 1 plate.
- Sloane, T.G. 1894. Studies in Australian entomology. No. VII. New genera and species of Carabidae. *Proceedings of the Linnaean Society of New South Wales* (2) 9: 393-455.
- \_\_\_\_\_. 1898. On Carabidae from West Australia, sent by Mr. A.M. Lea. *Ibid.* 23 (3): 444-520.
- \_\_\_\_\_. 1917. Carabidae from tropical Australia. *Ibid.* 42: 406-443.
- \_\_\_\_\_. 1920. The Carabidae of Tasmania. *Ibid.* 45: 113-180.
- \_\_\_\_\_. 1923. The classification of the Family Carabidae. *Transactions of the Royal entomological Society of London*, 1923, pp. 234-250.
- Straneo, S.L. 1943. Su alcuni Carabidi del Museo Civico di Genova faccolti in Africa occidentale da L. Fea. *Annali del Museo di Storia Naturali di Genova* 62: 55-61.
- Tanner, V.M. 1927. A preliminary study of the genitalia of female Coleoptera. *Transactions of the American Entomological Society* 53: 5-50, 15 plates.

## INDEX TO NAMES OF TAXA

(Synonyms in italics)

## FAMILY GROUP TAXA

Agrina, 112  
 Anomotarina, 110, 173  
 Apenina, 99, 112, 120, 124  
 Calleidina, 99, 110, 111, 112, 173  
 Calleiditae, 109, 116  
 Callidi, 110  
 Carabidae, 103  
 Catascopi, 109, 110  
 Catascopina, 110  
 Colliurini, 101  
 Coptoderitae, 109  
 Cymindidae, 101  
 Cymindina, 96, 98, 99, 108, 109, 110, 112,  
     129, 132, 133, 138, 158, 173, 197  
 Cymindini, 132, 158  
 Cyminditae, 109, 132  
 Demetriina, 110, 112  
 Dromii, 109, 110  
 Dromiina, 99, 110, 112, 196, 197  
 Dromiitae, 109, 196  
 Gallerucidiini, 111  
 Lachnophorini, 98, 101, 102, 103  
 Lebidii, 109, 111  
 Lebidiina, 110  
 Lebii, 109  
 Lebiidae, 109, 196  
 Lebiides, 101, 109, 110  
 Lebiina, 110, 116  
 Lebiinae, 158, 196  
 Lebiini, 96, 98, 101, 102, 108, 109, 110,  
     111, 116, 120, 196  
 Lebiitae, 109  
 Lichnasthenini, 99, 197  
 Lionychidae, 109, 196  
 Nemotarsina, 112  
 Pericalides, 109, 110  
 Pericalina, 98, 110, 111, 116, 197  
 Pericalitae, 109  
 Physoderi, 109  
 Physoderina, 110  
 Platynina, 98, 99  
 Pseudomasoreini, 132, 158

Pterostichini, 98, 99, 102  
 Singilini, 99, 196, 197  
 Somotrichini, 197  
 Thyreopteridae, 109, 116  
 Thyreopteritae, 109  
 Thysanotini, 98, 116  
 Zuphiini, 98, 99, 201

## GENERA AND SUBGENERA

Abaditicus, new subgenus, 99, 186, 187,  
     189, 190, 191  
 Afrotarus Jeannel, 99, 139, 145, 146, 149,  
     154, 156  
 Agastus Schmidt-Goebel, 99, 201  
 Agra Fabricius, 108, 109, 111, 129, 191  
*Anarmosta* Péringuey, 98, 99, 101  
 Anchonoderus Reiche, 102  
 Anomotarus (*sensu stricto*), 193, 196  
 Anomotarus Chaudoir, 173, 186, 192, 193,  
     196  
 Antimerina Alluaud, 98, 116  
 Apenes (*sensu stricto*), 125, 126  
 Apenes LeConte, 98, 99, 103, 124, 125,  
     126, 129, 132, 135  
 Apristus Chaudoir, 196  
 Asklepia Liebke, 101, 102, 103  
*Aspastus* Péringuey, 171  
 Assadecma Basilewsky, 99, 129, 133, 158,  
     170  
 Assadera Mandl, 157  
*Assotatus* Péringuey, 171  
*Assoterus* Péringuey, 171  
*Astus* Péringuey, 171  
 Callidomorphus Péringuey, 99, 197, 200  
 Calybe Castelnau, 101  
 Celaenephes Schmidt-Goebel, 112, 196  
*Cephalotarus* Mateu, 173, 193  
 Ceylonitarus, new genus, 99, 129, 132,  
     135, 138, 145  
 Charopterus Motschulsky, 200  
 Coptoptera Chaudoir, 99, 197, 201  
 Cymindis (*sensu stricto*), 132, 133, 135,  
     149, 156, 157

- Cymindis Latreille, 99, 109, 120, 127, 129,  
 132, 135, 138, 139, 145, 146, 149, 154,  
 156, 157  
 Cymindoidea (*sensu stricto*), 125, 126,  
 127, 128, 129, 133  
 Cymindoidea Castelnau, 99, 124, 126,  
 127, 128, 129  
 Diabaticus Bates, 99, 173, 186, 187, 188,  
 189, 190  
*Diaphoronus* Chaudoir, 172  
 Didymochaeta Chaudoir, 99, 125, 126  
 Dromiotes Jeannel, 173, 193  
 Dromius Bonelli, 109  
 Eucaerus (*sensu stricto*), 102, 107  
 Eucaerus LeConte, 98, 101, 102, 103, 107,  
 108  
 Eucheila Dejean, 109  
*Euplenes* Darlington, 99  
 Euplynes Schmidt-Goebel, 98, 99, 101  
 Euproctinus Leng and Mutchler, 111  
 Eurycoleus Chaudoir, 111  
 Gallerucidia Chaudoir, 111  
 Habutarus, new subgenus, 99, 124, 125,  
 126, 127, 128, 129  
 Haplopeza Boheman, 101  
 Hystrichopus (*sensu stricto*), 120, 145,  
 171, 172  
 Hystrichopus Boheman, 99, 129, 132, 133,  
 135, 138, 145, 157, 158, 170, 171, 173  
 Inna Putzeys, 109  
 Iscariotes Reiche, 157  
*Klepsiphrus* Péringuey, 201  
 Kleptoromimus Péringuey, 158  
 Klepturus Péringuey, 158  
 Lachnaces Bates, 98, 101, 102, 103, 107,  
 108  
 Lachnophorus Dejean, 101  
 Lebia Latreille, 109  
 Lebidia Morawitz, 111  
 Leptosarcus Péringuey, 99, 116, 120  
 Leptotrachelus Latreille, 101  
*Lestianthus* Sloane, 193  
 Lithostrotus Blackburn, 173, 192, 193  
 Madecassina Jeannel, 98, 116  
*Malisus* Motschulsky, 99, 125, 126  
 Menas Motschulsky, 156  
 Metaxymorphus (*sensu stricto*), 197, 200  
 Metaxymorphus Chaudoir, 99, 197, 200,  
 201  
 Mormolyce Hagenbach, 109  
 Nemotarsus LeConte, 108  
 Neopsammoxenus Emetz, 157  
*Nominus* Motschulsky, 125  
 Nototarus Chaudoir, 192, 193, 196  
*Notoxena* Chaudoir, 186, 187  
 Paracymindis Jedlička, 157  
 Periphobus Péringuey, 99, 197, 200  
 Phaedrusicum Liebke, 98, 101, 102, 103  
 Philophuga Motschulsky, 110  
*Philotecnus* Mannerheim, 126  
*Phloeocarabus* Macleay, 99, 186, 187, 188  
 Phloeoxena Chaudoir, 120  
 Pinacodera Schaum, 96, 99, 129, 132, 135,  
 139, 145, 149, 203  
 Plagiopyga Boheman, 99, 129, 132, 133,  
 135, 145, 157, 158, 172, 173  
 Planesus Motschulsky, 139  
*Platytarus* Fairmaire, 99, 124, 125, 126,  
 127, 129  
 Psammoxenus Chaudoir, 157  
 Pseudocymindis Habu, 157  
 Pseudomasoreus Desbrochers des Loges,  
 99, 129, 132, 133, 157, 158, 159, 164,  
 167, 168, 169, 170, 173  
 Pseudomastes Emetz, 157  
 Pteroritzella Mandl, 157  
*Selenorites* Jeannel, 116  
 Selenoritus Alluaud, 98, 116, 117  
*Speotarus* Moore, 173, 186, 187, 191, 192  
 Sphalera Chaudoir, 99, 124, 125, 126, 129  
*Sphenopalpus* Blanchard, 125  
*Sphenopselaphus* Gemminger and Harold,  
 125  
*Syndetus* Péringuey, 99, 201  
 Taridius Chaudoir, 99, 129, 133, 135, 139,  
 145, 146, 149  
 Tarulus Bedel, 157  
 Tecnophilus Chaudoir, 110  
 Thyreopterinus Alluaud, 98, 116, 117, 118  
 Thyreopterus (*sensu stricto*), 118  
 Thyreopterus Dejean, 98, 116, 117  
 Thysanotus Chaudoir, 98



Trigonothops (*sensu stricto*), 186, 187,  
188, 192  
Trigonothops Macleay, 99, 147, 173, 186,  
187, 188, 190, 191, 192  
Trymosternus Chaudoir, 99, 121, 124,  
126, 128, 129  
*Uvea* Fauvel, 192  
*Xatis* Fairmaire, 99

## SPECIES AND SUBSPECIES

aenea Dejean, *Cymindis*, 125  
alluaudi (Jeannel), *Thysanotus*, 116  
andrewesi (van Emden), *Cymindis*, 146,  
147, 148  
*andrewesi* van Emden, *Taridius*, 147  
angusticollis (Sloane), *Anomotarus*, 196  
angusticollis Boheman, *Hystrichopus*, 157  
arizonensis Horn, *Cymindis*, 157  
atriceps Péringuey, *Metaxymorphus*, 201  
australis (Erichson), *Trigonothops*, 188,  
189, 190  
*australis* Chaudoir, *Nototarus*, 192  
australis Erichson, *Diabaticus*, 186, 189  
*australis* Erichson, *Plochionus*, 186, 189  
badestrinus Bates, *Eucaerus*, 108  
basilewskyi, new species, *Hystrichopus*,  
164, 168  
birmanica (Bates), *Cymindis*, 146, 147,  
148  
*birmanicus* Bates, *Taridius*, 147  
bisignata Dejean, *Cymindoidea*, 126  
borealis LeConte, *Cymindis*, 157  
brunnea Chaudoir, *Coptoptera*, 201  
*callidoides* Chaudoir, *Euplynes*, 99, 101  
*canigoulensis* Fairmaire and Laboulbène,  
*Cymindis*, 157, 158  
*canigoulensis* Fairmaire and Laboulbène,  
*Pseudomasoreus*, 158, 159  
capicola (Basilewsky), *Hystrichopus*, 159,  
164, 167, 173  
capicola Basilewsky, *Pseudomasoreus*, 167  
ceylonicus, new species, *Ceylonitarus*, 135,  
138, 139  
*coerulescens* Blackburn, *Anomotarus*, 196

*coerulescens* Blackburn, *Lithostrotus*,  
192, 193  
collaris (Blackburn), *Trigonothops*, 188,  
190, 191  
*collaris* Blackburn, *Diabaticus*, 186, 189,  
190  
confusus Basilewsky, *Metaxymorphus*,  
201  
confusus Basilewsky, *Periphobus*, 201  
cordatus Rambur, *Trymosternus*, 128  
cursor Péringuey, *Metaxymorphus*, 201  
cyanipennis Schmidt-Goebel, *Euplynes*, 99  
cyclogonus Chaudoir, *Hystrichopus*, 173  
cymindoides Péringuey, *Hystrichopus*, 173  
*discopennis* Motschulsky,  
*Metaxymorphus*, 200  
*dispar* Péringuey, *Anarmosta*, 99, 101  
*dispar* Péringuey, *Euplynes*, 101  
dorsalis Thunberg, *Hystrichopus*, 172  
elegans Alluad, *Antimerina*, 116  
*famini* Dejean, *Cymindis*, 126  
*ferox* Péringuey, *Periphobus*, 197, 200,  
201  
*ferruginea* Boheman, *Plagiopyga*, 157,  
201  
flaviceps Motschulsky, *Metaxymorphus*,  
200  
*frenatus* Dejean, *Dromius*, 197  
*fuscata* Dejean, *Cymindis*, 139  
geminatus Bates, *Eucaerus*, 108  
haitianus Darlington, *Eucaerus*, 108  
*hamigera* Chaudoir, *Didymochaeta*, 125  
hessei Basilewsky, *Leptosarcus*, 120  
hieronticus Reiche, *Cymindis*, 156, 157  
hilaris Bates, *Eucaerus*, 108  
humeralis Fourcroy, *Buprestis*, 139  
insularis Darlington, *Eucaerus*, 108  
*jeanneli* Mateu, *Anomotarus*, 193  
kilimana Kolbe, *Cymindis*, 139, 154, 155,  
156  
kivuanus Basilewsky, *Hystrichopus*, 159,  
164, 167, 168  
kivuanus Basilewsky, *Pseudomasoreus*,  
167  
kivuanus Basilewsky, *Thyreopterus*, 118  
lebioides Bates, *Eucaerus*, 108

- leleupi* (Basilewsky), *Cymindis*, 154, 155  
*limbata* Dejean, *Cymindis*, 139, 149  
*longiplaga* Chaudoir, *Trigonothops*, 191  
*lucidula* Dejean, *Cymindis*, 125  
*lucifugus* Moore, *Speotarar*, 186  
*lucifugus* Moore, *Trigonothops*, 191  
*maculipennis* Mateu, *Cephalotarar*, 193  
*madagascariensis* (Basilewsky),  
*Hystrichopus*, 170, 172  
*madagascariensis* Basilewsky, *Assadecma*,  
158  
*mastersi* MacLeay, *Phloeocarabus*, 186  
*mateui*, new species, *Hystrichopus*, 164,  
169, 170  
*meruana* (Basilewsky), *Cymindis*, 154  
*meyeri*, new species, *Trigonothops*, 188,  
189, 190, 191  
*nigra* (Andrewes), *Cymindis*, 154, 155,  
156  
*nigricollis* MacLeay, *Trigonothops*, 186,  
187, 188  
*nigripes* Fairmaire, *Xatis*, 99  
*nilgirica* (Andrewes), *Cymindis*, 146, 147,  
148  
*nilgircus* Andrewes, *Taridius*, 147  
*nimbanus* Basilewsky, *Hystrichopus*, 172  
*olisthopoides* Bates, *Eucaerus*, 108  
*onychina* Dejean, *Cymindis*, 128  
*onychinus* (Dejean), *Trymosternus*, 128  
*opacicollis* Bates, *Eucaerus*, 108  
*opacula* (Chaudoir), *Cymindis*, 146, 147,  
148  
*opaculus* Chaudoir, *Taridius*, 139, 147  
*pacifica* Erichson, *Calleida*, 186  
*papua* (Darlington), *Cymindioidea*, 128  
*papua* Darlington, *Nototarar*, 127  
*parallelus* Blanchard, *Sphenopalpus*, 125  
*pauper* (Blackburn), *Trigonothops*, 188,  
189  
*pauper* Blackburn, *Diabaticus*, 189  
*planior* Blackburn, *Lithostrotus*, 196  
*platicollis* Say, *Cymindis*, 139, 149  
*porrectus* Péringuey, *Leptosarcus*, 120  
*postica* Dejean, *Cymindis*, 125  
*princeps* (Moore), *Trigonothops*, 192  
*ptolemaei* Alluaud, *Selenoritus*, 116, 117  
*ptolemaei* Alluaud, *Thyreopterus*, 118  
*pugnax* Péringuey, *Klepsiphrus*, 201  
*pulchripennis* Bates, *Eucaerus*, 108  
*punctigera* (LeConte), *Cymindis*, 189  
*punctulata* Dejean, *Cymindis*, 125  
*raffrayi* Fairmaire, *Cymindis*, 154, 155,  
156  
*reticulatus*, new species, *Hystrichopus*,  
159, 164  
*rufipes* Dejean, *Hystrichopus*, 172  
*scotti* Basilewsky, *Cymindis*, 154, 155  
*sculpturatus* Sloane, *Lestianthus*, 196  
*sericatus*, new species, *Eucaerus*, 107, 108  
*sericeus* Bates, *Eucaerus*, 107, 108  
*sericeus* Bates, *Lachnaces*, 107  
*simplex* Péringuey, *Syndetus*, 201  
*sinuata* (Say), *Cymindis*, 125  
*stevensi* (Andrewes), *Cymindis*, 139, 146,  
147, 148  
*stevensi* Andrewes, *Taridius*, 147  
*stigma* Mannerheim, *Philotecnus*, 126  
*stigmula* Chaudoir, *Anomotarar*, 193  
*stigmula* Chaudoir, *Cymindis*, 192  
*stigmula* Fairmaire, *Lebia*, 193  
*strandii* Liebke, *Asklepia*, 102, 103  
*striatus* Bates, *Eucaerus*, 108  
*sulcatus* Bates, *Eucaerus*, 108  
*suturalis* Dejean, *Cymindis*, 156, 157  
*suturalis* Liebke, *Phaedrusium*, 103  
*thoracicus*, new species, *Hystrichopus*,  
164, 167, 169, 170  
*titschacki* Liebke, *Phaedrusium*, 103  
*truncatus* Rambur, *Trymosternus*, 128  
*tumidiceps* Blackburn, *Anomotarar*, 196  
*uluguruanus* Basilewsky, *Hystrichopus*,  
159, 164, 167, 168  
*uluguruanus* Basilewsky, *Pseudomasoreus*,  
168  
*ustulatus* Gestro, *Agastus*, 201  
*varicornis* LeConte, *Eucaerus*, 107  
*variegata* Dejean, *Cymindis*, 125  
*vittiger* Chaudoir, *Metaxymorphus*, 197,  
201

### Book Review

Malicky, H. 1983. Atlas of European Trichoptera/ Atlas der europäischen Köcherfliegen/ Atlas des Trichoptères d'Europe. Series Entomologica 24, x + 298 pp. Dr. W. Junk Publishers, The Hague, Boston, London. ISBN 90-6193-134-7. Dfl. 175.00 (\$US 76.00 approx.).

The word 'European' in the context of the title of this book refers to a trichopteran faunal region which includes Europe, parts of the U.S.S.R. east of the Urals, Iran, Saudi Arabia, and Africa north of the Sahara desert. Text is minimal: there are no keys or descriptions. This picture book provides a basis for rapid identification of adults from the geographic area embraced.

Illustrations consist of standard aspects of male and female genitalia, and individual sclerites of the reproductive organs for all taxa, and of wing venation and other structures of some taxa. Information about other structures (i.e., presence or absence of ocelli, number of spurs, *et cetera*) is provided in coded form adjacent to the illustrations for each species, as is information about geographical distribution.

The coding system is explained with examples on page 3, and a table of symbols (as distinct from numbers also used for some parts) is given on each end-paper.

Formal keys are not provided, but a table on page 2 that functions as a key indicates distribution among taxa of character states of spur formula, ocelli, and number of segments of the maxillary palpus. This provides a quickly perceived entry to those sections of the illustrations which deal with particular genera, and portions of particular families. For the Limnephilidae, a similar table on page 151 indicates distribution among taxa of character states of the spur formula.

The text, contained on pages v- x, is entitled 'How to use this book', and is repeated in English, German, and French. It is written in telegraphic style. Other than this text, all explanations of symbols or the encoding of data accompanying illustrations is also in these three languages, and in the sequence mentioned above.

The book closes with: 1) references to sources of illustrations either taken directly from the publication, or of which the originals were borrowed; 2) a taxonomic index to families and genera.

Illustrations of species are organized by family and genus, and by species group for the more highly diverse genera. Also, for the more highly diverse genera, illustrations of females are grouped separately from those of males. Each group of illustrations is headed by the appropriate generic and familial name, and on the same line is given coded information about the taxon in question. This line is set off by an underline that extends with the width of the page. Each species is identified by specific epithet, author, year of original publication, and some coded information, all on one line. Drawings are from various sources, and many are accompanied by arrows or pointers which indicate key characters to observe in identification. This is similar to the system used in the Peterson field-guide series to indicate such features.

To the following points I take exception.

1). As all illustrations are not Malicky's, they are presented in a multiplicity of styles. This jars the sense to some extent, and makes for potential difficulty in comparison of species, a point made by Malicky in the introduction. A single style would have been preferable. However, this would have required a single artist, and the resulting delay in completion of the illustrations would have delayed for a long time completion of the book.

2). I can foresee that users of this book will wield their pencils busily, marking off the limits of illustrations of one species from those of another. This will not be required throughout, but I

note some pages on which it is difficult to tell where illustrations for one species end and those of the next begin.

3). In at least the more highly diverse (e.g. *Rhyacophila* and *Limnephilus*) illustrations of females are placed together, several pages away from those of the males. I would have preferred to have illustrations of both sexes of each species together. However, I recognize that there are advantages to grouping illustrations by sex rather than by species.

4). A system of symbols, however simplified, is a barrier to understanding, until it has been thoroughly learned. Thus, it might have been preferable to use a less telegraphic way of presenting the information about taxa. However, Malicky's system of symbols renders the information available to three linguistic communities, using a minimum of space.

5). I dislike the practice of having generic names and specific epithets in the same typeface as all other print in the book because I have difficulty in distinguishing these names for what they are. Thus, use of italics would have been preferable for scientific names.

6). Within the more highly diverse genera, the species are arranged in species groups. This is appropriate for making comparisons. However, given the separation of illustrations of structures of males and females, and given that females do not necessarily show in their features sufficient community for similar groupings, it is difficult to locate the appropriate female illustrations to go with the male. One has to search each and every name on the pages with illustrations of females to make the necessary associations. Provision of a simple index of specific epithets would have obviated this difficulty.

7). The species within species groups ought to have been arranged alphabetically. Although the names of genera are not arranged alphabetically, an appropriate index is provided.

8). On page 3 (on which lay-out of coded information for each genus or species is explained), I find it irritating that two examples are given of the use of a family name, followed by a generic name, and that genus does not belong in that family! These are: LEPIDOSTOMATIDAE: PLECTROCNEMLIA, and MOLANNIDAE: LARCASIA. It seems more appropriate to use correct information for examples.

These faults do not detract from the importance and value of this book. Malicky states that this is not a review of classification of the European Trichoptera, but rather the first compendium prepared since McLachlan's work of the 1870's. It is indeed a worthy, though rather different, successor to McLachlan's publication.

This book will be of use to all those who study the European fauna of aquatic insects: ecologists, ethologists, morphologists, and, not least, taxonomists. These workers require accurate identifications of caddis fly adults, and this book, used with care, makes such identifications possible. For those who are not primarily specialists on the European fauna, the book will provide the basis for obtaining a general notion of diversity of European caddis flies, and structural divergence of the adults.

Physically, the book is of larger size than is usual. It is hardbound, set up in signatures and properly stitched for durability. The paper is clear white, strong, and unglazed (thus, no glare from the surface).

Given today's prices, the cost is reasonable in terms of what one is getting.

A. P. Nimmo  
Department of Entomology  
The University of Alberta  
Edmonton, Alberta, Canada













Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required: one in English, and one in another language, preferably French.

Tables, including titles and footnotes, must not be more than 7 3/4 X 4 3/4 inches (19.7 X 12.1 cm). Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 3/4 X 5 inches, or 19.7 X 13.2 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, \$17.00 per volume of four issues, normally appearing at quarterly intervals; single issues \$5.00. Back volumes and issues are available at the same cost. There is a postal surcharge of \$4.00 to subscribers outside Canada. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to:

The Editor, *Quaestiones Entomologicae*  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3

4/6/1  
6/13  
5/17

# Quaestiones Entomologicae

Edmonton

1988

1988

A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.



A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 19

Numbers 3-4

1983

## CONTENTS

Goulet—The Genera of Holarctic Elaphrini and Species of <i>Elaphrus</i> Fabricius (Coleoptera: Carabidae); Classification, Phylogeny and Zoogeography . . . . .	219
Book Review—Chvála, M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families of Hybotidae, Atelestidae and Microphoridae. . . . .	483
Book Review—Duval, C. T. (Series Editor). 1982. Fauna of New Zealand. . . . .	486
Book Review—Griffiths, G. C. D. (Editor). 1982. Flies of the Nearctic Region. . . . .	489
Book Review—Halffter, G. and W. D. Edmonds. 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae)—an Ecological and Evolutive Approach . . . . .	491
Editor's Acknowledgements . . . . .	494
Index to Volume 19 . . . . .	495







*Elaphrus olivaceus* LeConte. 1863. Female, dorsal aspect. Length of body 7.6 mm. Illustration by D. R. Maddison.



THE GENERA OF HOLARCTIC ELAPHRINI AND SPECIES OF *ELAPHRUS*  
FABRICIUS (COLEOPTERA: CARABIDAE): CLASSIFICATION, PHYLOGENY AND  
ZOOGEOGRAPHY.<sup>1</sup>

Henri Goulet

Biosystematics Research Institute

Agriculture Canada

K.W. Neatby Bldg., Ottawa, Ontario K1A 0C6

*Quaestiones Entomologicae*

19: 219-482 1983

ABSTRACT

*The tribe, genera, and subgenera of Elaphrini are redefined on characters of adults and larvae. Recognized are three genera of Elaphrini, (Diacheila Motschulsky, Blethisa Bonelli, and Elaphrus Fabricius), four subgenera of Elaphrus Fabricius, (Arctelaphrus Semenov, Neolaphrus Hatch, Elaphrus, and Elaphroterus Semenov), 34 species and 3 subspecies of Elaphrus. Keys to genera of Elaphrini and to subgenera, species and subspecies of Elaphrus are given for adults and known larvae.*

*Four species are described as new: E. lindrothi (type locality: United States: Illinois, Jackson Co., 3 mi. N. Pomona), E. marginicollis (type locality: United States: Colorado, Jack's Gulch, Roosevelt N.F.), E. mimus (type locality: United States: California, Angwin), and E. comatus (type locality: China, Heilung Kiang, Harbin). The following synonymies are proposed for the first time: Elaphrotatus Semenov 1895 = Elaphroterus Semenov 1895; Elaphrus ruscarius foveatus Pierce 1948 = Elaphrus finitimus Casey 1920; Elaphrus clairvillei lynni Pierce 1948 = Elaphrus clairvillei Kirby 1837.*

*Treatment of each species includes: synonymic list, diagnostic combination and description of adults and larvae, discussion of variation, derivation of the specific epithet, geographic distribution, collecting notes, taxonomic notes, and geographical affinities. Important character states are illustrated. Geographical distributions are mapped for all North American species of Elaphrus. Results of statistical analyses of geographic variation of each species are discussed.*

*Relationships of genera and subgenera of Elaphrini are established using separate procedures of phenetic and cladistic systematics, based independently on characters of adults and larvae. A phylogeny is reconstructed for genera of Elaphrini, and for subgenera and species of Elaphrus based on structural characters of adults and larvae.*

*It is postulated that the ancestral elaphrine stock evolved and radiated in tropical Asia where it became extinct except for the immediate ancestor of the elaphrines surviving in the temperate zone of northernmost Siberia and Alaska in the Late Cretaceous. There, it radiated and gave rise to ancestors of extant genera and subgenera. The history of elaphrine evolution is a succession whereby ancestral peripheral elements extend into areas of low diversity followed by radiation. This pattern was repeated with the formation of the cold temperate,*

---

<sup>1</sup>Modified and expanded from a thesis submitted to the University of Alberta in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

boreal and arctic zones.

## RÉSUMÉ

A l'aide des caractères morphologiques de l'adulte et de la larve, la tribu, genres et sous-genres des *Elaphrini* sont définis de nouveau. Nous reconnaissons trois genres à l'intérieur de la tribu (*Diacheila* Motschulskay, *Blethisa* Bonelli et *Elaphrus* Fabricius), quatre sous-genres à l'intérieur du genre *Elaphrus* (*Arctelaphrus* Semenov, *Neoelaphrus* Hatch, *Elaphrus*, et *Elaphroterus* Semenov), ainsi que 34 espèces et 3 sous-espèces du genre *Elaphrus*. Nous présentons des clefs de détermination pour les adultes et larves connues des genres d'*Elaphrini*, ainsi que des sous-genres, espèces et sous-espèces d'*Elaphrus*.

Quatre nouvelles espèces pour la science sont décrites: *E. lindrothi* (localité-type: Etats Unis: Illinois, Comté de Jackson, 5 km au nord de Pomona) *E. marginicollis* (localité-type: Etats Unis: Colorado, Jack's Gulch, Forêt Nationale de Roosevelt), *E. mimus* (localité-type: Etats Unis: Californie, Angwin), et *E. comatus* (localité-type: Chine: Heilung Kiang, Harbin). Les synonymes suivants sont proposés pour la première fois: *Elaphrotatus* Semenov 1895 = *Elaphroterus* Semenov 1895; *Elaphrus* ruscarius foveatus Pierce 1948 = *Elaphrus* finitimus Casey 1920; *Elaphrus* clairvillei lynni Pierce 1948 = *Elaphrus* clairvillei Kirby 1837. Pour chaque espèce traitée dans ce travail, les informations suivantes sont incluses: liste des synonymes, diagnose et description de l'adulte et de la larve, discussion de la variation géographique, origine des noms nouveaux proposés, répartition géographique, notes sur l'habitat et la biologie, notes taxonomiques et affinités géographiques. Les caractères morphologiques importants sont illustrés de même que la répartition géographique des espèces néarctiques du genre *Elaphrus*. Les résultats de l'analyse statistique de la variation géographique de chaque espèce sont également discutés.

Les relations d'affinité entre les genres et sous-genres d'*Elaphrini* ont été établies à partir des techniques phénétiques et cladistiques, basées indépendamment sur les caractères morphologiques de l'adulte et de la larve. Nous présentons également un arbre phylogénétique des genres d'*Elaphrini* et des sous-genres et espèces d'*Elaphrus* établi à l'aide des caractères de l'adulte et de la larve.

Nous croyons que la lignée ancestrale des *Elaphrini* s'est développée et répandue en Asie tropicale pour ensuite y disparaître sauf pour l'ancêtre immédiat des *Elaphrini* qui a probablement survécu dans les régions tempérées de la Sibérie septentrionale et de l'Alaska à la fin du Crétacé. Cet ancêtre par la suite a évolué dans cette région et donné naissance aux lignées ancestrales des genres et sous-genres actuels. L'histoire évolutive des *Elaphrini* est perçue comme une succession d'invasions d'éléments périphériques vers des régions de faible diversité suivie de spéciation. Ce patron s'est répété lors de la formation des régions tempérées, boréales et arctiques.

## TABLE OF CONTENTS

Introduction	221
Materials and Methods	222
Materials	222
Methods	225
Tribe <i>Elaphrini</i>	230
Key to Genera of <i>Elaphrini</i>	232
Genus <i>Diacheila</i> Motschulsky	235
Genus <i>Blethisa</i> Bonelli	236
Genus <i>Elaphrus</i> Fabricius	238
Key to Subgenera of <i>Elaphrus</i> Fabricius	239
Subgenus <i>Arctelaphrus</i> Semenov	241
Subgenus <i>Neoelaphrus</i> Hatch	246
Key to Species of Subgenus <i>Neoelaphrus</i> Hatch	247
Subgenus <i>Elaphrus</i> Fabricius	282
Key to Species of Subgenus <i>Elaphrus</i> Fabricius	284
Subgenus <i>Elaphroterus</i> Semenov	322
Key to Species and Subspecies of Subgenus <i>Elaphroterus</i> Semenov	323
Notes on Structures Correlated with Cryptic Coloration of Adults of <i>Elaphrus</i> with Their Substrate.	375

Phenetics and Cladistics: Larvae and Adults .....	376
Phylogeny of Elaphrini .....	445
Classification of Elaphrini .....	451
Zoogeography of Elaphrini .....	452
Concluding Remarks .....	465
Acknowledgements .....	465
Literature Cited .....	466

## INTRODUCTION

Since capturing my first specimen of *Elaphrus* in 1962, I have remained excited by these beetles. Adults of most species are beautifully sculptured, and some are brilliantly coloured. Moreover, the marked specialization in habitat requirements of many species fascinated me (Goulet, 1964).

Adults of *Elaphrus* are easy to recognize because of their cicindeloid shape, and four rows of large elytral depressions (pits). Unfortunately many species of the subgenus *Elaphrus* are difficult to characterize. However, Lindroth, (1961) in his revision of North American species, laid the groundwork for further studies.

This work is intended as a continuation of Lindroth's work. I deal with intraspecific variation, larvae, behaviour, and habitat requirements. Although I focus much of my efforts on North American species, I include all Palaearctic taxa known to me. I gathered large amounts of structural evidence about adults and larvae to test separate phylogenetic reconstructions for congruence, and to help students of fossil insects working with fragments of specimens. More detailed descriptions are in my thesis (1978, University of Alberta, Edmonton, Canada). Finally, I attempt to trace past zoogeographical events.

*Cicindela riparia* Linnaeus, 1758, was the first formally recognized species of *Elaphrus*. Fabricius (1775) erected the genus *Elaphrus* to include the above species, and others that are today in *Notiophilus* Duméril, 1806, and *Bembidion* Latreille, 1802. Latreille (1810) designated *E. riparius* as type species, and excluded *Bembidion* from *Elaphrus*. Dejean (1826) published the first revision and restricted *Elaphrus* to its present concept. Some authors after Dejean used the genus *Elaphrus* in a wider sense: Brullé (1834) included *Pelophila* Dejean, 1828, and *Blethisa* Bonelli, 1810; Lacordaire (1854) added *Opisthius* Kirby, 1837. However, Dejean's concept became generally accepted.

Semonov (1895, 1926), who was studying the rich Russian *Elaphrus* fauna, recognized the natural species-groups of *Elaphrus*, and arranged the species in five subgenera.

Larvae were first described by Schiødte (1867). Major advances in knowledge of larvae were made by van Emden (1919, 1942), Lindroth (1954) and Luff (1976). Presently all elaphrine genera and subgenera can be recognized in larval stages.

In a few recent works, precise habitats of many species were described (Lindroth, 1949, 1961). Bauer (1973, 1974 and 1976) provided much insight about behaviour, ecological relationships and dispersal potential of some species of *Elaphrus*.

I hope that my work will not only make possible identification of specimens, but also stimulate more detailed investigations into the many problems in evolutionary biology that render members of this genus so interesting. Thus, I have attempted to solve some of the many problems in speciation of North American *Elaphrus*, to improve classification of the Palaearctic *Elaphrus* complex, and to point out many other problems that demand particular

attention.

## MATERIALS AND METHODS

### Materials

I based this study on about 18,000 adults (1500 Palaearctic) and 400 larvae (20 Palaearctic). Most adults were loaned to me by various institutions and private collectors in Canada, United States and Europe. Larval material came mostly from my collection (all *ex ovo*, C.H. Lindroth (Sweden) and T. Bauer (Austria). Fossil fragments from Pleistocene and Miocene deposits were provided by J.M. Matthews, A.A. Morgan, A. Ashworth and R.E. Morlan. The following abbreviations, mostly from Arnett (1969), represented these collections and their respective curators.

- ALAR A. Larochelle, Collège Bourget, C.P. 1000, Rigaud, Québec. J0P 1P0.
- AMNH Department of Entomology Collection, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024; L.H. Herman.
- ANSP Department of Entomology Collection, Academy of Natural Sciences, 19th and Parkway, Philadelphia, Pennsylvania 19103; M.G. Emsley.
- BMCS Musée d'Histoire Naturelle de Bale, Bale, Suisse; W. Whittmer.
- BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW.7 5BD, England; R. Aldridge.
- BMSC Buffalo Museum of Science, Humbolt Park, Buffalo, New York 14211; H.W. Charnley.
- BMUW Burke Museum, Department of Zoology, University of Washington, Seattle, Washington 98105; M.H. Hatch.
- CASC Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; D.H. Kavanaugh.
- CDAE Bureau of Entomology, State of California, Department of Agriculture, 1220, N. St., Sacramento, California 95814; T. N. Seeno.
- CISC California Insect Survey, Division of Entomology and Acarology, University of California, Berkeley, California 94720; J.A. Chemsak.
- CJEA C. Jeanne, Bordeaux, France.
- CNCI Canadian National Collection of Insects, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario K1A 0C6; A. Smetana.
- CSLB Entomological Collections, California State College at Long Beach, Long Beach, California 90801; E.L. Sleeper.
- CUIC Cornell University Insect collection, Department of Entomology, Cornell University, Ithaca, New York 14850; L.L. Pechuman.
- CWSC Canadian Wildlife Service Collection, Ottawa, Ontario K1A 1C7; R.I.G. Morrison.
- DEFW Department of Entomology, Fisheries and Wildlife Collection, University of Minnesota, St. Paul, Minnesota 55101; P.J. Clausen.
- DEUN Department of Entomology Collection, University of Nebraska, Lincoln, Nebraska 68503; B.C. Ratcliffe.
- DHKA D.H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

- DMNH Dayton Museum of Natural History, 2629 Ridge Ave., Dayton, Ohio 45414; E. J. Koestner.
- DRWH D.R. Whitehead, Agriculture Research Service, c/o United States National Museum, Washington, District of Columbia 20560.
- DZEC Department of Zoology and Entomology Collection, Montana State University, Bozeman, Montana 59715; N.L. Anderson.
- EJKC E.J. Kiteley, 16-13th Street, Roxboro 900, Québec.
- EMUS Entomology Museum, Department of Zoology, Utah State University, Logan, Utah 84321; W.J. Hanson.
- ESUW Entomology Section Museum, Plant Sciences Division, University of Wyoming, Laramie, Wyoming 83070; R.J. Lavigne.
- FGAC F.G. Andrews, Department of Food and Agriculture, 1220 N. Street, Sacramento, California 95814.
- FMNH Division of Entomology Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605; H.S. Dybas.
- FNYS F.N. Young, Department of Zoology, Indiana University, Bloomington, Indiana 47401.
- FRLC Forest Research Laboratory Collection, Box 4000. Fredericton, New Brunswick; E3B 5P7; G.R. Underwood.
- HGOU H. Goulet, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario K1A 0C6.
- HHCC H. Hacker, 235 Randall St., San Francisco, California 94131.
- ICCM Section of Insects and Spiders, Carnegie Museum, Pittsburgh, Pennsylvania 15213; G.E. Wallace.
- INHS Insect Collection, Illinois State Natural History Survey, Urbana, Illinois 61803; M.W. Sanderson.
- ISUI Department of Zoology and Entomology Collection, Iowa State University, Ames, Iowa 50010; J.L. Laffoon.
- JBEL J. Belicek, Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3.
- JMCI J.M. Cicero, 13641, Terrace Bella St., Pacoima, California 91331.
- JSCC Joe Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.
- JVMA J.V. Matthews, Jr., Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario K1A 0E8.
- KSUC Department of Entomology Collection, Kansas State University, Manhattan, Kansas 66502; H.D. Blocker.
- LACM Insect Collection, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007; C.L. Houes.
- LSUC Department of Entomology Collection. Louisiana State University. Baton Rouge, Louisiana 70803; J.B. Chapin.
- MCPM Milwaukee City Public Museum, 800 West Wells St., Milwaukee, Wisconsin 53233; K.W. MacArthur, G.R. Noonan.
- MCZC Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J.L. Lawrence.
- MSUC Department of Entomology Collection, Michigan State University, East Lansing, Michigan 48823; E.R. Hoebeke.

- NCSU Department of Entomology Collection, North Carolina State University, Raleigh, North Carolina 27607; D.A. Young.
- NDSU Entomology Department Collection, North Dakota State University, Fargo, North Dakota 58102; R.L. Post.
- NMDC N.M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.
- NSMC Insect Collection, Nova Scotia Museum, Halifax, Nova Scotia B3H 3A6; L. Martin.
- OSEC Department of Entomology Collection, Oklahoma State University, Stillwater, Oklahoma 74074; W.A. Drew.
- OSUC Ohio State University Collection of Insects and Spiders, 1735 Neil Ave., Columbus, Ohio 43210; C.A. Triplehorn.
- PADA Insect Collection, Bureau of Plant Industry, Pennsylvania Department of Agriculture, 2301 North Cameron St., Harrisburg, Pennsylvania 17120; T.J. Henry.
- PMNH Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; K.W. Brown.
- PSUC Department of Entomology Collection, Pennsylvania State University, University Park, Pennsylvania 16802; K.C. Kim.
- PURC Entomology Research Collection, Department of Entomology, Purdue University, Lafayette, Indiana 47907; A. Provonsha.
- RFCC R. Freitag, Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1.
- ROMC Royal Ontario Museum, University of Toronto, Toronto 5, Ontario M5S 2C6; G.B. Wiggins.
- SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044; P.D. Ashlock.
- SFAC Department of Biology Collection, Stephen F. Austin State College, Nacogdoches, Texas 75961; W.W. Gibson.
- TBAU T. Bauer, I. Zoologisches Institut der Universität Wien, Austria.
- UADE Department of Entomology Collection, University of Arkansas, Fayetteville, Arkansas 72701; E.P. Rouse.
- UASM Department of Entomology, Strickland Museum, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.
- UBCZ Spencer Entomology Museum, Department of Zoology, University of British Columbia, Vancouver 8, British Columbia V6T 1W5; G.G.E. Scudder.
- UCDC Department of Entomology Collection, University of California, Davis, California 95616; R.O. Schuster.
- UCEC Department of Entomology Collection, University of Colorado, Boulder, Colorado 80302; U.N. Lanham.
- UCRC Department of Entomology Collection, University of California, Riverside, California 92502; S.I. Frommer.
- UICM Department of Entomology Collection, University of Idaho, Moscow, Idaho 83843; W.F. Barr.
- ULIC Department of Biology Insect Collection, University of Louisville, Louisville, Kentucky 40208; C.V. Covell.

- UMMZ Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104; R.S. Alexander.
- UMRM Entomology Research Museum, 1-87 Agriculture Building, University of Missouri, Columbia, Missouri 65201; W.R. Enns.
- USNM Division of Coleoptera, Department of Entomology, United States National Museum of Natural History, Washington, District of Columbia 20560; P.J. Spangler.
- UVCC Department of Zoology Collection, University of Vermont, Burlington, Vermont 95401; R.T. Bell.
- UWOC Department of Zoology Collection, University of Western Ontario, London Ontario N6A 5B7; W.W. Judd.
- UWEM Entomology Museum, Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706; W.J. Bayer.
- UMKC V.M. Kirk, Northern Grain Insect Research Laboratory, Brookings, South Dakota 57006.
- UZMF Universitetes Zoologiska Museum, Entomologiska Avdelningen, N. Jarnvagsgatan 13, SF-00100 Helsingfors 10, Finland; H. Silfverberg.
- WSUC Department of Entomology Collection, Washington State University, Pullman, Washington 99163; M.T. James.
- ZMLS Zoological Institute, Department of Systematics, University of Lund, Lund, Sweden; C.H. Lindroth.

### Methods

*Collection of Specimens.*— Adults of all species of *Elaphrus* live along rivers, small streams, swamps, sloughs, or bogs. On substrates of rough organic texture, beetles were taken by treading the vegetation under water. On substrates of fine texture (clay, fine muds), treading was done slowly and gently moving in one direction to force the beetles out of cracks before being trod upon and buried (in cloudy or rainy weather, I do not tread as most beetles of these habitats are inactive then and so will be buried).

In moist but not soggy bogs, where the vegetation could not be trod under water, pitfall traps were most productive. I used pitfall traps successfully in all habitats where *Elaphrus* live. In wet habitats, I used a modified pitfall trap requiring no digging. This trap consists of a 25 cm trough with a gentle sloping ramp allowing beetles to climb up to the trap edge. The latter is rounded rather than sharp to increase efficiency of the trap.

Larvae live in the same habitat as that of adults, but different procedures were used to collect them. Some larvae enter pitfall traps, but a more fruitful method was to gently press by hand the organic surface many times at the same spot. This yielded numerous larvae especially those of the first instar. On fine textured soil or inorganic habitats, repeated splashing with water yielded larvae.

*Preservation and preparation.*— Adults were killed and stored in ethyl acetate fumes, or were killed and preserved in 70% ethanol (voucher specimens for reared larvae and for dissection). After cleaning, the specimens were mounted on points. Larvae were killed in almost boiling water (heat destroys autolytic enzymes and fixes, after three to five minutes, the body in a straight position) and stored in 70% ethanol, or were killed and stored in 70% ethanol. After cleaning, some larvae were dehydrated (freeze-, critical point-, or chemical-drying) and others were mounted in glycerine so that body proportions were preserved, and the specimen could be

studied and moved easily and viewed from different angles. An efficient glycerine mount can be achieved as follows:

1. If a preserved larva is 5 to 10 mm long, pierce the thorax ventrally or laterally. If larger (10 to 20 mm) pierce the abdomen and enlarge the opening. This facilitates the next step.
2. Place the larva in gently boiling 10% KOH for 3 to 5 minutes.
3. Transfer the larva into distilled water with a wide mouthed eye-dropper to avoid collapsing the body. Neutralize the remnants of KOH by changing most of the water several times.
4. Transfer the larva with wide mouthed eye-dropper into 4% glycerin-water solution (V/V). The best receptacles are concave at the bottom.
5. Place the receptacle on a microscope slide drying plate where water will evaporate (60°C). Add more of the glycerin solution after a few hours. Twelve hours or less is enough to complete the glycerin concentration and impregnation process. The larvae are then ready to be transferred to a ringed slide for study, or to closed vials of glycerin for storage. If larvae are studied at magnifications below 200X, it is not necessary to use cover slips if glycerin is levelled with upper edge of the ring. This greatly facilitates positioning of specimens. The ring should be made of a material that is chemically stable, or the larvae should be on the slide for less than a month.

### Rearing of Larvae

Techniques for rearing elaphrines as well as other carabids were previously described (Goulet, 1976). Larvae of most North American *Elaphrus* were reared from eggs (except *E. lapponicus* Gyllenhal, *E. marginicollis* new species, *E. mimus* new species, *E. viridis* Horn and *E. parviceps* Van Dyke). Larvae of last four species are not known, but those of *E. lapponicus* were recognized by association with adults (Lindroth, 1954). In addition, I studied larvae reared from eggs of four palaearctic species (*E. cupreus* Duftschmid, *E. riparius* (Linnaeus), *E. aureus* Müller, and *E. ulrichi* Redtenbacher). I reared from eggs larvae of *Diacheila polita* Faldermann, *Blethisa multipunctata* (Linnaeus) and *B. quadricollis* Halderman. I also studied larvae of *B. julii* LeConte recognized by association with adults (Lindroth, 1954).

### Descriptive Format

The descriptive format for adults closely matches that of Whitehead (1972). Among larval instars, many characters remain unmodified (position of basic setae and pores, relative length of basic setae), but others are variously modified (microsculpture of sclerites and membrane, and number of accessory setae). The first instar larvae have peculiar characters (egg-bursters, lack of subapical and sublateral bead on the mesonotum, the metanotum and the terga 1 to 8, lack of accessory setae). Second instar larvae differ from those of the third instar in the number of accessory setae. Therefore, characters of all larvae are given under the description of "First instar larva"; those peculiar to the second instar are given under "Second instar larva"; and those of the third instar relative to those of previous instar larvae are given under "Third instar larva".

In "Taxonomic notes" I refer to number of males dissected. This number represents only the specimens for which the complete median lobe and parameres were studied. The character states of the parameres and the base of the median lobe are generally not used at specific level. However, the apex of the median lobe is an important character at the specific level, and has been examined in about 5% of males.



Descriptions of genera, subgenera and species are organized according to the postulated phylogeny starting with earliest lineages.

### External Structures of Adults and Larvae

Basic external structures of adults were described by Lindroth (1969), and those of larvae by van Emden (1942). In the following discussion, unusual structures are briefly defined.

Sculpture of an elytron of *Elaphrus* consists of four rows of circular pits (depressions) and one to four rows of mirrors (strongly reflecting surfaces) (Figs. 111, 113). At the middle of each pit (except the two subhumeral pits) there is a setigerous puncture (Fig. 123). In adults of some species, the lateral edges of pits are delimited by curved ridges, in those of other species, by impressions only. Mirrors are distinctly outlined if the punctures around them are sharply separated from the mirror surface, but indistinctly outlined if the punctures are progressively more scattered toward the middle of the mirror. Mirrors are contrasted if the color of the mirror is clearly different from nearby surface color, or if nearby surface is microsculptured and dull. In this study, I retraced the origin of striae and intervals. The rows of pits and mirrors are in intervals 3, 5, 7 and 9, and areas between rows of pits are in intervals, 1, 2, 4, 6 and 8.

Setae in immatures are of two types; basic and accessory. Basic setae are found on the first instar larvae. Accessory setae on the second and third instar larvae are setae in addition to those of the first instar larvae. On larvae, pores are small circular hole-like depressions the size of a setigerous puncture. Only basic setae and pores of larvae are coded.

Except for setae on the legs, setae on adults are well understood and few in number. Thus, no special name was given to them.

In larvae, setae and pores are numerous and important in systematics. Thus, a preliminary notation system was designed. I use similar designations for apparently homologous setae and pores. This system is based on the setae and pores of first instar larvae. Those added in the second and third instars are not part of this notation system as they vary in position and number. This basic system of setae and pores, based on elaphrines, seems to be a common feature of larvae of most Carabidae. I do not follow Habu's (1961) system for head setae, as it is incomplete.

Designation of setae and pores is derived from their position. The first part of the designation denotes the position of a small group of setae and pores, and the second part, the position of the seta or pore inside the group, *i.e.*, seta PII-P of pronotum refers to a submedial group (PII) posteriorly, and to a posterior seta (-P) in the group (Fig. 76c). I did not homologize setae and pores on abdominal terga 9 and 10, and on sternum 10 with those of other abdominal segments. Codes for setae and pores are illustrated in Fig. 76a-g.

Microsculpture of adults and larvae varies considerably. Microsculpture, in this work, refers to small microscopic features about 5 to 10 microns in length. These features may be outlined by meshes (microscopic grooves). The meshed microsculpture may be roughly circular (termed isodiametric) or variously stretched (termed transverse) (Fig. 151), and its surface may be flat, subconvex, convex, scale-like, cone-like, seta-like etc. Most types of microsculpture studied are without meshes. The shapes of these features are named in relation to well known analogous objects, *i.e.*, single-pointed (tooth-like), multi-pointed (row of teeth), and others mentioned above (Figs. 152-156).

Punctures are important surface features of adults of *Elaphrus*. Punctures are circular to elongate in outline. Their diameter is expressed as the longest axis in microns (average values given in text). Their density is expressed as distance, in microns, between nearest margin of two

punctures (average values given in the text).

Most features of male genitalia have established terms. However, the enormous strut derived from the internal sac and extended through the basal orifice of the median lobe is called the stylet (Fig. 39).

I follow Noonan's (1973) terms for the ovipositor except for the two markedly sclerotized structures that form the stylus (Fig. 71). These sclerites are respectively the basal and apical sclerites. I failed to find distinguishing characters between genera in the spermatheca and its glands.

### **Mensural and Nominal Character States**

These data were obtained for adults with a Leitz stereoscopic microscope at magnifications of 12.5, 18, 50, 72, 150 and 216 diameters using a micrometer eyepiece with a scale interval of 0.05 mm at 18 diameters.

The following abbreviations indicate the measurements made on each selected specimen:

EL –Elytral length from apex of scutellum to apex of elytron.

EW –Elytral maximum width.

PL –Pronotal length from basal margin to anterior margin along the longitudinal median stria.

PW –Pronotal maximum width.

HW –Maximum head width between the external margins of the eyes.

These measurements were used unmodified, or in ratio combinations for statistical analysis, as follow: PL/PW, PL/EL, PL/EW, PL/HW, PW/EL, PW/EW, PW/HW, EL/EW, EL/HW, EW/HW.

Atchley et al. (1976) question the use of ratios in statistical analyses, as the denominator variable of a ratio is still correlated (depending on the coefficient of variation of each variable) with the ratio. Ideally, analyses should be done with raw data by proper methods (*i.e.*, principal components and multivariate analyses), as done in some analyses with complex problems (Goulet and Baum 1981, 1982). However, ratios are easily understood by most readers, and are wisely used in infraspecific analyses as independant variables.

Measured characters were analyzed statistically. Nominal and meristic character states were expressed only as means, because the variance is much too high for interpretation (Mayr, 1969).

### **Descriptive Statistics**

Except for one North American and one Palaearctic species each known from two specimens only, I present descriptive statistics of at least one sample of each species. For samples of eight specimens or more, I provide the following statistics of dispersion: range of variation, mean, two standard errors of the mean, 1.5 standard deviations, and coefficient of variation (Mayr, 1969). Briefly, four standard errors difference between means of two samples signify that the probability of these means being the same is only 5%, or insignificant. Thus, such difference is regarded as statistically significant. If two populations differ in a character measured by 3.0 standard deviations (assuming normal distribution), then 90% or more of the specimens in one sample are likely to be different from 90% or more of the specimens in the other sample. Such a difference is regarded as taxonomically significant at the subspecies level. When the difference observed is statistically significant, it is referred as "significant"; but when it is taxonomically distinct, it is referred as "taxonomically significant".

I followed Whitehead (1972) in determining sample size and its assembly. Ideally, 10 males and 10 females collected in one locality at one time were used. If necessary, specimens from localities in geographically homogeneous areas were assembled to make a sample. With rare species, I used all specimens available.

Despite differences usually between means of males and females, data for each variable of both sexes are pooled. Differences in their means for linear measurements are below 5%, and those for ratios less than 1%. In this work, linear measurements are not generally significant in taxonomic analyses (see under *E. lapponicus*), but ratios are widely used in infraspecific analyses as evidence for gene flow between proximate samples. While pooling slightly increased the coefficient of variation, more was gained with larger samples in defining the mean of each variable.

### Illustrations

Line drawings were made with assistance of an ocular grid in a Leitz stereoscopic dissecting microscope. For complex structures, or surface microscopic features, I used photographs taken with a Scanning Electron Microscope.

I provide maps of the distributions of all North American species, and present a brief description of ranges of Palaearctic species. Special maps were prepared to illustrate some clinal relationships and broad zoogeographic patterns.

### Taxonomic Methods

*Sorting of Taxa.*— Adults of *Elaphrus* were first sorted according to Lindroth (1961) for North American species, to Semenov (1895), Ganglbauer (1892), Palmén (1944) and Lindroth (1939) for European species, and to Semenov (1889, 1895, 1897, 1904a, 1926) and Ohkura (1973) for Asiatic species. Then, I arranged the material of these taxa geographically for more refined intrapopulation analyses.

*Criteria for Species, Subspecies.*— A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley, 1978). In this study preserved specimens were used, and evidence for reproductive isolation is suggested by structural gaps between clusters of similar individuals.

Subspecies are geographically delimited populations, actually or potentially connected by gene flow. The subspecies category is reserved for populations in relatively advanced stages of speciation. In such populations, a large portion of genes will present a modified allelic distribution as well as new alleles. Such differences, if reflected phenotypically, provide the basis for subspecies recognition. This category is used when 90% or more of specimens of one population differ from those of the other.

When in doubt about populations being subspecies, vernacular names (e.g. Coastal form, Mount Rainer form) are used to simplify discussion and encourage further investigation of these geographical units.

Evidence of divergence between two geographically proximate samples is not considered proof of lack of gene flow between them. Evidence from additional neighbouring samples must also be considered. If the most geographically proximate samples of two allopatric groups of populations are most similar, or show no sign of divergence among characters studied, it was concluded that gene flow potentially or actually exists, and thus the groups are conspecific. If the most geographically proximate samples are the most divergent or are divergent in one or

more characters, it was concluded that gene flow is probably interrupted currently and two possibilities emerged. Either these samples show evidence of gene flow through neighbouring samples, in which case they are considered conspecific, or they do not, in which case they are subspecifically or specifically distinct.

Like Whitehead (1972), I found that the most meaningful statistical approach was to compare means of geographically proximate samples rather than other statistical parameters. These statistics suggest whether or not the differences between means are probably the results of coincidence.

## CLASSIFICATION

### TRIBE ELAPHRINI

- Elaphrii Latreille, 1802:81 (*ex parte*). 1804:213. 1806:177, 227. Fairmaire and Laboulbène, 1854:6 (*ex parte*). Schaum, 1856:59 (*ex parte*).
- Elaphrini Erichson, 1837:4 (*ex parte*). Schiødte, 1841:351 (*ex parte*). Letzner, 1849:50. Leconte, 1861:7. Redtenbacher, 1874:5 (*ex parte*). Dalla-Torre, 1877:22 (*ex parte*). Horn, 1881:104, 110. Bedel, 1881:21. Fauvel, 1882:23, 80. LeConte and Horn, 1883:10. Seidlitz, 1891:24, 19. Ganglbauer, 1892:121. Reitter, 1908:72, 75, 96. 1909:104. Blatchely, 1910:48. Kuhnt, 1912:49. Schaufuss, 1916:6, 29. Porta, 1923:42. Sloane, 1923:243. Portevin, 1929:40. Joy, 1932:328. La Rivers, 1946:138. Hatch, 1953:62. Lindroth, 1954:3. Ball, 1960:106. Lindroth, 1961:101. Lindroth, 1969a: XVIII, XXI. Lindroth, 1974:32.
- Elaphri LeConte, 1853:401.
- Elaphrides Lacordaire, 1854:41,43 (*ex parte*).
- Elaphrites Jacquelin du Val, 1857:5 (*ex parte*).
- Elaphrina Thomson, 1859:192. Sahlberg, 1880:10. Jacobson, 1906:266.
- Elaphridae Marseul, 1880:29. Jeannel, 1941:212. Jeanne, 1966:16.
- Elaphrinae Okhura, 1973:4. Freude, 1974:81.

### Adults

*Diagnostic combination.*— Unique among adults of other tribes as in following. Metasternum with inverted V-shaped micropunctate or punctate impression medially; metepimeron present and very narrow (in some specimens fused to metepisternum); lateral ridge under elytron with apical file of longitudinal keel-like sculpture; tergum 7 with lateral pair of plates expanded apically into curved row of points; clip setae of fore-tibia curved and not sinuate.

*Description.*— Medium-sized to large (length of body 6.0 to 18.0 mm).

*Head.* Two pairs of supraorbital setae.

*Mandible* (Figs. 1-3) with one seta dorso-laterally in anterior third of mandibular scrobe. Outer margin of maxilla (Figs. 5-7) with three setae on basal 0.5 of stipes; palpifer with two setae on outer margin; palpomere 1, 0.4 to 0.5 as long as palpomere 2; palpomere 2, 1.5 to 1.75 as long as palpomere 3; palpomere 3, 0.5 to 1.0 as long as palpomere 4. Labium (Fig. 8) with one pair of subapical setae; paraglossae narrow, serrated on inner margin, and in most species exceeding apex of ligula; palpiger with one small ventro-basal seta; palpomere 2 with two setae. Mentum with one or two pairs of setae; medial tooth emarginate. Submentum with six or eight setae subapically.

*Thorax.* Pronotum with two setae on lateral margin (one pair near middle and one near hind angle), with one seta near hind angle, or setae lacking. Forecoxal cavities closed behind, and midcoxal cavities disjunct (*i.e.*, adjoining mesepimeron). Metasternum with inverted V-shaped micropunctate or punctate impression medially.

*Elytron.* Striae (9) of elytron completely developed, partly obsolete laterally, traceable at base, or lacking; base of stria 5 more deeply impressed basally. Basal projection of elytron with two to seven oval punctures. Setigerous punctures present on interval 9 (roughly equidistant), on scutellar stria (one puncture), on intervals 3, 3 and 5, or 3, 5 and 7. Ventral surface of elytron with longitudinal keel-like microsculpture near apex (Lindroth, 1954).

*Wing.* Very similar among elaphrine genera (Fig. 32).

*Abdomen.* Tergum 7 with fan-like plates laterally; posterior margin of plate with 11 to 25 sharp points (Gahan, 1900; Lindroth, 1954); terga 6 and 7 with a pair of basal microtrichial fields; microtrichial fields of tergum 7 extended to posterior margin. Sterna 5 and 6 with transverse basal sulcus; sterna 4, 5 and 6 with one pair of large medial setae, and sternum 7 with one or two pairs of seta on posterior margin.

**Legs.** Foreleg (Figs. 145 and 146). Trochanter with one, two or three setae. Tibial spurs distant, therefore, tibia of anisochaetous type and close to grade B type (for terms see Hlavac, 1971); setal band with vertical section and long (30% of tibia length, medial expansion present but not shifted far anteriorly); antennal channel shallow and developed far posteriorly to clip setae; different from grade B type in lacking confluent zone between setal band and dorsal inner fringe (ASR of Hlavac, 1971); clip setae curved but not sinuate; dorsal inner fringe dense, extended along apical 0.3 to 0.7 of tibia. First three or four tarsomeres of males slightly to moderately enlarged and with ventral spongy pubescence, or narrow and without ventral spongy pubescence.

**Midleg** (Figs. 147 and 148). Coxa with one, two or numerous setae. Trochanter with one, two or three setae, or setae lacking.

**Hindleg.** Coxa with one large seta and with one to 40 smaller setae. Trochanter with six to twelve spinules on posterior margin at base.

**Male genitalia.** Parameres subequal; left paramere wider than right one; ventral margin of both parameres with two rows of setae; setae extending almost to base. Opening of internal sac dorsal and subapical; interior of sac with microtrichia, brushes, fields of scales; posterior portion of sac protruding posteriorly beyond basal orifice of median lobe; protruded portion stylet-like and formed by three sclerites surrounding ejaculatory duct; ejaculatory duct inserted into stylet subapically.

**Ovipositor.** Stylus with basal and apical sclerites. Apical sclerite without or with one or two apical setae (Fig. 70).

## All Instar Larvae

**Diagnostic combination.**— Recognized from larvae of other tribes as in following. Head not constricted at base, at most with shallow emargination of lateral margin between eye and base; cervical, ventro-lateral, supra-ocular and postero-ocular groove lacking; nasale pointed medially; projection of adnasale posterior to medial point of nasale; epicranial suture present. Antennae as short as mandibles. Mandible with penicillus on basal inner margin and with small seta on outer margin at level of retinaculum. Lacina conical or barely developed; seta of lacinia apical or subapical. Terga small, exposing epipleurites in dorsal view; urogomphus unarticulated, relatively slender, about as long as tergum 10. Seta of claw very short.

## First Instar Larvae

**Description.**— Body length 4–8 mm.

**Head.** (Figs. 87 to 92). Egg-bursts parallel, black, keel-shaped, and extended below level of seta EM-P. Nasale pointed medially; teeth absent or very small to large. Adnasale projected moderately or slightly. Suture of frontale bisinuate. Epicranial suture 0.2 to 1.0 as long as antennal scape. Eyes with six stemmata. Antennomere 1 equal or 1.2 as long as antennomere 2, antennomere 3, 0.7 to 1.5 as long as antennomere 2, antennomere 4, 0.7 as long as antennomere 3.

**Mouthparts.** Mandibles sickle-shaped and with single retinaculum; penicillus on basal inner margin, and with four to seven closely associated small setae; outer margin with small seta at level of posterior margin of retinaculum. Outer margin of stipes (Fig. 83) with two large setae, one in anterior and one in posterior 0.3; inner margin of stipes with small seta posterior to lacinia; inner half of dorsal surface of stipes with 30 to 50 setae; ventral surface of stipes with one small seta near inner margin; stipes with three pores ventrally: one posterior to palpus, one centrally in basal 0.3, and one more baso-laterally. Palpomere 1 about 2.0 as long as palpifer, palpomere 2, 1.0 to 1.5 as long as palpomere 1, palpomere 3, 0.5 to 0.7 as long as palpomere 2; palpifer with small ventro-medial seta. Galea with two subequal galeomeres; galeomere 1 with ventro-subapical seta, galeomere 2 with one baso-medial and one medial microseta; seta on lacinia small or very small. Prementum (Fig. 82) dorsally with one pair of very small setae latero-subapically, and one pair of small setae medio-laterally, ventrally with one pair of very small setae baso-sublaterally. Labial palpus with two subequal palpomeres; palpomere 2 fusiform.

**Thorax.** Pronotum (Fig. 76c) with medial sulcus; disc darkly sclerotized; epipleuron, anterior and posterior bands thinly sclerotized; anterior band and epipleuron sharply delineated from disc, posterior band diffusely delineated; anterior and posterior bands and basal portion of epipleuron with vermiculate black pigment; anterior band with irregular longitudinal channels; lateral margin of disc without bead; disc with weakly transverse furrow, furrow ending near level of setal system ME. Prosternite strongly sclerotized, but anterior half weakly sclerotized; disc with one postero-medial pair of setae and with five to seven pairs of very small setae sublaterally. Poststernite with one seta.

Mesonotum (Fig. 76c) shorter than pronotum; medial suture present; lateral transverse sulcus absent; anterior margin beaded; epipleuron and posterior band weakly sclerotized, anterior band lacking; epipleuron sharply and posterior band diffusely delineated from disc. Mesosternite with one pair of setae. Metathorax similar to mesothorax except sculpture slightly more expanded, and anterior margin not beaded.

Membranous surfaces with pointed microsculpture over most of surface.

**Abdomen.** Terga 1 to 8 (Fig. 76e) with medial suture, terga 9 and 10 entire; tergum 1 widest, maximum width of each tergum tapering toward tergum 9; urogomphi as long as tergum 10, unarticulated, moderately slender, and in dorsal view

curved inward (Figs. 93a, 95 and 98a); apex of tergum 10 with two pairs of eversible sacs (one dorso-medial and one ventro-lateral pair) covered with hook-like microsculpture; terga 1 to 10 without defined anterior band or epipleuron; posterior band present on terga 1 to 9, indistinctly delineated from disc, more weakly sclerotized, with vermiculate black pigment, and without irregular longitudinal channels. Hypopleuron present on segments 1 to 8, fused to sternum on segment 9, and without setae or pores. Anterior sternite of abdomen present on segments 1 to 8, fused to sternum 9, and with one very small seta. Sternite and posternites separated on segments 1 to 7, and fused together on segments 8 to 10; sternite on segments 1 to 8 with one pair of setae, sternite 9 without setae. Inner poststernite with two setae. Outer poststernite with two setae except on segment 1 with anterior seta only.

*Legs.* Tarsus with one pair of subequal claws; claw with one very small seta.

**Second Instar Larvae**

*Description.*— Linear measurements about 1.5 times as long as those of first instar larvae of same species. Numerous accessory setae present over most sclerites in addition to basic setae and pores.

*Head.* Ventral surface of parietale with two fields of isodiametric or slightly transverse sculpture, one medial and one lateral to systems VMM and VMP. Egg-bursters lacking.

*Thorax.* Anterior band of pronotum and prosternum with irregular longitudinal channels on disc. Posterior margin of prosternum beaded. Subapex of mesonotum with transverse bead extended antero-sublaterally. Anterior sternite of mesothorax with one to three accessory setae. Metathorax as above but pointed sculpture slightly more expanded and accessory setae slightly more numerous in most species. Pointed micro-sculpture widespread on membranous surfaces.

*Abdomen.* Terga 1 to 8 with transverse bead extended sub-basally and sublaterally; posterior band with or without irregular longitudinal channels; urogomphus with 14 to 50 setigerous punctures.

**Third Instar Larvae**

*Description.*— Linear measurements about 1.5 times longer than those of second instar larvae of same species. Accessory setae of most sclerites more numerous than those of second instar larvae of same species.

**Geographical Distribution and Affinities, and Notes**

*Distribution.*— Species of this tribe live in all regions of the northern hemisphere (except for Greenland and Iceland) from the southern edge of the tundra to the southern half of the temperate zone (southern California, northernmost Florida, Morocco). Few species occur in subhumid regions and none are found in desert regions.

NOTES ABOUT KEYS

Larvae are best studied in glycerin. They may also be studied in alcohol, though many characters are not readily seen. Setae are divided into four size classes: very small, small, medium-sized and large. Examples of these size classes are shown on the maxilla (Fig. 83b). I provide five keys: one to genera, one to subgenera of *Elaphrus* and three to species of these subgenera. Lindroth (1954) provided means of identification for known adults and larvae of species of *Diacheila* and *Blethisa*.

**Key to genera of Elaphrini**

**Adults**

- 1      Lateral margin of pronotum with two pairs of setae (one near middle and one near hind angle). Elytral striae well developed on disc (Figs. 28, 29 and 30); setigerous punctures present on elytral intervals 3,5 and 9 or 3 and 9. Middle coxa with one or two setae. Eyes small or moderate; medial margins lower than frons ..... 2
- 1'     Lateral margin of pronotum with one pair of setae near hind angle or setae

lacking. Elytral striae barely suggested near base or absent (Figs. 110 to 117); setigerous punctures present on elytral intervals 3, 5, 7 and 9. Middle coxa with numerous setae. Eyes large; medial margins higher than frons

- ..... *Elaphrus* Fabricius p. 238
- 2 (1) Lateral portion of pronotum not explanate. Elytral interval 3 not catenate (Fig. 28); setigerous punctures present on elytral intervals 3 and 9. Fronto-ocular sulcus very shallowly impressed and linear (Fig. 14). Clypeus without impression. Mentum with one pair of setae (Fig. 8) ..... *Diacheila* Motschulsky p. 235
- 2' Lateral portion of pronotum explanate. Elytral intervals 3 and 5 catenate (Figs. 29 and 30); setigerous punctures present on elytral intervals 3, 5 and 9. Fronto-ocular sulcus sharply impressed and eight-shaped (Fig. 15). Clypeus with sublateral impressions. Mentum with 2 pairs of setae (Fig. 9) ..... *Blethisa* Bonelli p. 236

#### All Instar Larvae

- 1 Lacinia well developed and cone-shaped (Figs. 83c and 84). Base of mandible narrow: basal inner margin apparently continuous with apical inner margin (Fig. 78) ..... 2
- 1' Lacinia suggested or absent (Figs. 85c and 86). Base of mandible wide: basal inner margin not in line with apical inner margin (Figs. 80 and 81) ..... *Elaphrus* Fabricius p. 238
- 2 (1) Teeth of nasale small (Fig. 87a). Ventral surface of stipes with membranous declivity laterally behind postero-lateral seta ..... *Diacheila* Motschulsky p. 235
- 2' Teeth of nasale large (Fig. 88b). Ventral surface of stipes completely sclerotized ..... *Blethisa* Bonelli p. 236

#### DISTINCTION OF SEX IN ADULTS

Adult males, except in those of *E. punctatus* which lack any secondary sexual characters, are recognized by enlarged basal tarsomeres of forelegs with white hair-like structures ventrally, termed spongy pubescence. In most species, males have a small tooth-like projection at the base of inner spur of the midtibia; in some species, males are more densely setose centrally on abdominal sterna than females; in a few species, males have tooth-like projections at base of apical spur and of posterior spur of foretibia, or only at base of posterior spur; in one species, males have a large ventral projection on forefemur.

#### DISTINCTION OF LARVAL INSTARS

Recognition of first larval instar is easy, but separation of the second from third instar larvae is difficult. Except for a greater number of accessory setae on most sclerites in the third instar than the second instar larvae of each species, no other differences were found. However, the number of accessory setae is different between species of the same instar. Therefore, the segregation of these instars of Elaphrini is possible only after determination of the genus and

subgenus. Fortunately, genera and subgenera are recognized by characters common to all instar larvae (see keys of genera of Elaphrini and subgenera of *Elaphrus* respectively on p. 233 and p. 240). The following key provides necessary information for segregating all instars of known species of elaphrine larvae. In couplet 2 locate the genus or subgenus of the specimen, then compare couplet 2 and 2' for this genus or subgenus. Characters in couplet 2 describe second instar larvae, and those in couplet 2', third instar larvae. Male and female larvae are not distinguishable by external structures.

**Key for recognition of larval instars**

- 1 Egg-bursters present as parallel black carinae sublaterally on frontale (Fig. 87). Mesonotum, metanotum and terga 1 to 8 without transverse submarginal bead along anterior and lateral margins (Figs. 76c, 76e). Only basic setae and pores present on sclerites as illustrated (Fig. 76). Urogomphus with five large and one very small setae . . . . . First instar
- 1' Egg-bursters absent from frontale. Mesonotum, metanotum and terga 1 to 8 with transverse submarginal bead along anterior and lateral margins. Many accessory setae present on most sclerites in addition to basic setae and pores of first instar. Urogomphus with seven to 30 major accessory setae (Figs. 93b, 94, 96, 98b, 99, 100, 101 and 103). Second or third instar . . . . . 2
- 2 (1') *Diacheila*. - Projections on urogomphus half as large as those of third instar larvae (Fig. 93b).  
*Blethisa*. - Pronotal epipleuron with 20 accessory setae or less, on mesonotal epipleuron with 15 or less, sternite of segments 2 to 7 with 40 or less, and outer poststernite of segments 2 to 7 with 10 or less.  
*Elaphrus (Arctelaphrus)*. - Head width 0.8 mm. (I have not seen the second instar larva, but number of accessory setae probably follows a pattern similar to members of subgenus *Elaphrus*, thus I assume the following would apply). Each sclerite of mesonotum and metanotum with 10 accessory setae or less, epipleuron of abdominal segments 2 to 8 with 10 or less, sternite of segment 9 without, and outer poststernite of segments 2 to 7 with five or less.  
*Elaphrus (Neoelaphrus)*. - Proepisternum with five accessory setae or less, each sclerite of mesonotum and metanotum with 15 or less, and outer poststernite of segments 2 to 7 with seven or less.  
*Elaphrus (Elaphrus)*. - Each sclerite of pronotum with 15 accessory setae or less, each sclerite of mesonotum and metanotum with 10 or less, each sclerite of terga 1 to 8 with nine or less, hypopleuron of abdominal segments 2 to 8 with four or less, and sternite of abdominal segments 2 to 8 with ten or less. Urogomphus with largest projection half as large as that on third instar larvae (Fig. 100).  
*Elaphrus (Elaphroterus)*. - Proepisternum with seven accessory setae or less, each sclerite of terga 1 to 8 with 30 or less, hypopleuron of abdominal segments 2 to 8 with eight or less, sternite of abdominal segments 2 to 8 with 14 or less, and outer poststernite of segments 2 to 7 with four or less



## Second instar

2' *Diacheila*. - Largest projection of urogomphus large (Fig. 94).

*Blethisa*. - Pronotal epipleuron with 30 accessory setae or more, each sclerite of mesonotum with 90 or more, mesonotal epipleuron with 20 or more, sternite of abdominal segments 2 to 7 with 90 or more, and outer poststernite of segments 1 to 7 with 30 or more.

*Elaphrus (Arctelaphrus)*. - Head width 1.1 mm. Each sclerite of mesonotum and metanotum with 16 accessory setae, epipleuron of abdominal segments 2 to 8 with 18, sternite of abdominal segment 9 with eight, and outer poststernite on segments 2 to 7 with seven.

*Elaphrus (Neoelaphrus)*. - Proepisternum with 25 accessory setae or more, each sclerite of mesonotum and metanotum with 25 or more, and outer poststernite of segments 2 to 7 with nine or more.

*Elaphrus (Elaphrus)*. - Each sclerite of pronotum, mesonotum and metanotum with 21 accessory setae or more, each sclerite of terga 1 to 8 with 17 or more, hypopleuron of abdominal segments 2 to 8 with eight or more, and sternites of abdominal segments 2 to 8 with 14 or more. Largest projection of urogomphus large (Fig. 100).

*Elaphrus (Elaphroterus)*. - Proepisternum with 10 accessory setae or more, each sclerite of terga 1 to 8 with 40 or more, hypopleuron of abdominal segments 2 to 8 with 12 more, sternite of abdominal segments 2 to 8 with 28 or more, and outer poststernite of segments 2 to 7 with seven or more .

..... Third instar

Genus *Diacheila* Motschulsky

Figs. 2, 5, 8, 14, 28, 38, 70, 78, 79, 83a-c, 84, 87a-b, 93a-b, 94

*Diacheila* Motschulsky, 1846:12. Type-species: *Harpalus arcticus* Gyllenhal, 1810, fixed by Lindroth (1961), by subsequent designation. Lindroth, 1961:102.

*Diaheila* Motschulsky, 1846:74. Lindroth, 1961:102 (invalid emendation).

*Diachila*; Motschulsky, 1846. Schaupp, 1878:29. Marseul, 1880:67. Horn, 1881:111 Marseul. 1882:4. LeConte and Horn, 1883:11. Jacobson, 1906:267. Lindroth, 1954:3, 4. Ball, 1960:106 (invalid emendation).

*Arctobia* Thomson, 1859:3, 194. Type-species: *Harpalus arcticus* Gyllenhal, 1810, fixed by Thomson (1859), by monotypy. Marseul, 1882:4. Lindroth, 1954:4.

## Adults

*Diagnostic combination*.— Distinguished from other elaphrine beetles by presence of setigerous punctures on intervals 3 and 9 only, and by dissociated striae 2 and 3 of elytron.

*Description*.— Medium-sized 7.0 to 9.0 mm.

*Head*. Eye moderate or small, medial margin lower than frons. Fronto-ocular sulcus very shallowly impressed (Fig. 14). Clypeus without impression. Apical retinacular and basal terebral tooth of right mandible small (Fig. 2). Maxillary palpomere 3, 0.5 as long as palpomere 4 (Fig. 5). Mentum (Fig. 8) with one pair of setae.

*Thorax*. Pronotum with lateral portion not explanate and with two pairs of setae; lateral bead narrow or wide. Scutellum without transverse ridge basally. Mesosternum without postero-lateral ridge. Posterolateral setae of metanotum very small.

*Abdomen*. Tergum 2 with one pair of postero-submedial ridge. Tergum 1 without setae. Abdominal sternum 7 with one pair of setae on posterior margin.

*Elytron*. Most striae clearly defined on disc; striae 2 and 3 dissociated from base to subapex (Fig. 28); interval 3 not catenate. Surface of intervals smooth near setigerous punctures and equally brilliant. Setigerous punctures small (20 microns), round, without antero-medial cuticular prominence, restricted to intervals 3 and 9; interval 3 and 9 respectively with four to seven and with six to ten setigerous punctures. Punctures restricted to striae.

*Wing.* Similar to that of species of *Blethisa* with rounded posterior end of oblongum (see Fig. 33).

*Legs.* Foreleg: trochanter with two setae, femur with 20 setae or less, fringe on medio-dorsal surface of tibial in apical 0.4 to 0.5. Midleg: coxa with two setae, trochanter with one seta, femur with 20 setae or less. Hindleg: coxa with three setae.

*Male genitalia.* Median lobe (Fig. 38) markedly sclerotized generally and becoming weakly sclerotized dorso-apically. Stylet of internal sac narrow, short, and not spatulate anteriorly.

*Ovipositor.* Basal sclerite of stylus with defined lateral and medial ridges dorsally, and with small setae on dorsal ridges and apico-ventral surface. Apical sclerite with few small setae, apex with two small setae (Fig. 70).

### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other elaphrine genera by well developed and conical lacinia (Figs. 83c and 84), and small teeth on nasale (Fig. 87b).

*Description.*— Ultimate length 7 to 10 mm. Medial portion of nasale slightly or moderately projected; teeth on nasale fine; base of mandible narrow, and basal inner margin seemingly continuous with apical inner margin. Lacinia well developed and conical; seta apical and small, or subapical and very small. Ventral surface of stipes with membranous declivity behind postero-lateral seta (Fig. 83b).

### Geographical Distribution and Affinities, and Notes

*Distribution.*— Species of this Holarctic genus live in subarctic and southern arctic regions, from Scandinavia through Siberia, and from Alaska to Labrador. One relict species occurs along the Tien-Shan mountains in Western China and neighbouring USSR (Lindroth, 1954).

*Taxonomic notes.*— Lindroth (1954) recognized three extant species. I studied in detail adults of two of them: *Diacheila arctica* Gyllenhal and *D. polita* Faldermann, and briefly those of *D. fausti* Heyden. I will not discuss the species further as Lindroth's review is most satisfactory. Lindroth (1954) described the larva of *D. arctica* and Sharova (1958) described that of *D. polita* (confirmed by my own rearing). I examined six first instar and three second instar larvae of *D. polita* from the Anderson River delta, NWT. I failed to locate the larva of *D. arctica* studied by Lindroth. Since the data on *D. arctica* were insufficient, I was unable to characterize more fully larvae of the genus; thus the description is only partially comparable with that of other genera.

### Genus *Blethisa* Bonelli

Figs. 1a-b, 6, 9, 15, 29, 30, 33, 39a-d, 71, 88a-b, 95, 96a-b

*Blethisa* Bonelli, 1810. Type-species: *Carabus multipunctatus* Linnaeus, 1758, fixed by Bonelli (1810), by monotypy. Dejean, 1826:3, 265. Dejean and Boisduval, 1830:119. Heer, 1838:39 (*ex parte*). Motschulsky, 1846:74. LeConte, 1850:208. 1853:401. Lacordaire, 1854:44 (*ex parte*). Schaum, 1856:75. Jacquelin du Val, 1857:6 (*ex parte*). Thomson, 1859:3, 194. LeConte, 1861:7. Crotch, 1873:4. Redtenbacher, 1874:6. Seidlitz, 1875:3. Dalla-Torre, 1877:23. Schaupp, 1878:29. Marseul, 1880:33 (*ex parte*). Horn, 1881:111. Bedel, 1881:21, 22. Fauvel, 1882:81, 85. Marseul, 1882:4. LeConte, 1883:11. Seidlitz, 1891:4, 19. Ganglbauer, 1892:121. Everts, 1898:48. Jacobson, 1906:266. Reitter, 1908:96,97. 1909:106. Blatchley, 1910:49. Kuhnt, 1912:31, 49. Fairmaire, 1913:30. Schaufuss, 1916:28,29. Porta, 1923:78. Portevin, 1929:41. Jacobson, 1931:82. Joy, 1932:328. Jeannel, 1941:215. Lindroth, 1954:3, 10. Ball, 1960:106. Lindroth, 1961:104. Ohkura, 1973:4. Lindroth, 1974:32.

*Helobium* Leach, 1815:83. Type-species: *Carabus multipunctatus* Linnaeus, 1758, fixed by Leach (1815), by monotypy. Lindroth, 1961: 104. Lindroth, 1974:32.

*Rhaphiona* Fisher von Waldheim, 1829:34. Type-species: *Blethisa eschscholtzi* Zoubkoff, 1829, fixed by Fisher von Waldheim (1829), by monotypy. Lindroth, 1961:104.

### Adults

*Diagnostic combination.*— Distinguished from other elaphrine beetles by deeply impressed fronto-ocular sulcus (shaped as a figure 8, see Fig. 15), by weakly impressed clypeus sublaterally, by long maxillary palpomere 3 (0.7 as long as palpomere 4), by two pairs of setae

on mentum, by explanate lateral portion of pronotum, by presence of setigerous punctures on elytral intervals 3, 5 and 9, and by one seta on femur of hind leg.

**Description.**— Medium to large beetles: 10 to 18 mm.

**Head.** Eye well developed, medial margin lower than frons. Fronto-ocular sulcus deeply impressed and shaped as a figure 8 (Fig. 15). Clypeus with weak sublateral impressions. Apical retinacular and basal terebral tooth of right mandible small or large, (Fig. 1). Maxillary palpomere 3, 0.7 length of palpomere 4 (Fig. 6). Mentum (Fig. 9) with 2 pairs of setae.

**Thorax.** Pronotum with lateral portion explanate and with two pairs of setae. Scutellum with transverse ridge basally. Postero-lateral ridge of mesosternum well developed. Postero-lateral setae of metanotum medium-sized.

**Abdomen.** Tergum 2 without postero-medial ridge. Tergum 1 with numerous setae. Abdominal sternum 7 with two pairs of setae on posterior margin.

**Elytron.** Striae 1-6 well defined, remaining striae slightly expressed, irregularly interrupted, or obsolete; intervals 3 and 5 catenate (Figs. 28, 29). Surface between two setigerous punctures brighter than that of proximate intervals (mirror-like), or not brighter; surface near setigerous puncture flat or elevated, but not pit-like. Setigerous punctures large (50 to 60 microns in diameter), antero-medially emarginated and elevated, restricted to elytral intervals 3, 5 and 9; interval 3 with five or six, interval 5 with two to four, and interval 9 with nine to nineteen setigerous punctures; setigerous punctures small. Punctures restricted to striae.

**Wing.** Similar to that of species of *Diacheila* with rounded posterior end of oblongum (Fig. 33).

**Legs.** Foreleg: trochanter with one seta, femur with 16 setae or less, fringe on medio-dorsal surface of tibia on apical 0.3. Midleg: coxa with one or two setae, trochanter with one or without setae, femur with 20 setae or less. Hing leg: coxa with two setae.

**Male genitalia.** Baso-lateral and ventral surface of median lobe markedly sclerotized, and sharply delimited from weakly sclerotized dorsal surface (Fig. 39). Stylet of internal sac large, protruded well beyond basal orifice, and spatulate anteriorly.

**Ovipositor.** Basal sclerite of stylus without lateral and medial ridges dorsally, and with numerous setae in apical 0.7 (Fig. 71). Apical sclerite with many very small spinules on surface, apex with two small setae.

## All Instar Larvae

**Diagnostic combination.**— Distinguished from the larvae of other elaphrine genera by large and conical lacina, and large teeth on nasale (Fig. 88b).

## First Instar Larvae

**Description.**— Ultimate length 7 to 10 mm. Medial portion of nasale obtusely pointed (Fig. 88a), teeth of nasale large and occupying all of anterior margin. Angle formed by seta DI-A and pores DI-P and DMP-E about 160°. Base of mandible narrow, and basal inner margin seemingly continuous with apical inner margin. Lacina large and conical; seta subapical and very small. Ventral surface of stipes completely sclerotized. Microsculpture of urogomphus scale-like.

## Second and Third Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of other genera by divided epipleuron on abdominal segments 1 to 8, and presence of accessory setae on the ventral surface of stipes.

## Second Instar Larvae

**Description.**— Ultimate length 9 to 15 mm. Accessory setae present on ventral surface of stipes. Each sclerite of pronotum and mesonotum respectively with about 95 and with 60 to 70 accessory setae. Abdominal epipleuron of segments 1 to 8 divided in two.

## Third Instar Larvae

**Description.**— Ultimate length 15 to 23 mm. Each sclerite of mesonotum with 90 to 110 accessory setae.

## Geographical Distribution and Affinities, and Notes

**Distribution.**— Species of this Holarctic genus are found in arctic, boreal and temperate regions, from the British Isles to Kamchatka, and from Alaska to Newfoundland (Lindroth, 1954).

*Taxonomic notes.*— Adults of species of this genus were revised by Lindroth (1954). Goulet and Smetana (1983) characterized one additional species and proposed a phylogeny and zoogeography for species of the genus.

Larvae of *B. multipunctata* and *B. julii* are similar. Characters presented in Lindroth's (1954) key are difficult to interpret or are variable. The larvae of these species are characterized as in the following. In larvae of *B. julii*, the apical teeth of nasale are fused into one large tooth (Lindroth, 1954:21, Fig. 11b) and the microsculpture is less developed on mesonotum and metanotum (pointed sculpture near suture is barely developed in second instar larvae, absent in third instar larvae, and suggested or absent antero-laterally). In larvae of *B. multipunctata*, the apical teeth of nasale are separated by a very small sharp tooth medially (Lindroth, 1954:21; Fig. 11c) and the microsculpture is more widespread on mesonotum and metanotum (pointed sculpture along suture forms a wide band in second instar larvae or a narrow band in third instar larvae, and is widely developed antero-laterally). This augments Lindroth's key (1954:23, 24).

I have seen adults of all species of *Blethisa* reviewed by Lindroth (1954). I examined four first instar, three second instar, and three third instar larvae of *B. quadricollis* Haldeman from the junction of the Athabasca River with Highway 2, Alberta; six first instar, two second instar, and three third instar larvae of *B. multipunctata* Linnaeus from George Lake, Alberta; five second instar larvae of *B. julii* LeConte from three localities in Newfoundland, and two third instar larvae of *B. julii* from two localities in Newfoundland.

### Genus *Elaphrus* Fabricius

*Elaphrus* Fabricius, 1775:227. Type-species: *Cicindela riparia* Linnaeus, 1758, fixed by Latreille (1810), by subsequent designation. Rossi, 1790:193. Olivier, 1790:4 (*ex parte*). Latreille, 1796:75 (*ex parte*). Illiger, 1798:225 (*ex parte*). Fabricius, 1801:245 (*ex parte*). Latreille, 1802:81 (*ex parte*). 1804:214. 1810:158 (*ex parte*). Gyllenhal, 1810:6 (*ex parte*). Dejean, 1826:3, 268. Curtis, 1827:19. Erichson, 1837:3. Dejean and Boisduval, 1830:124. Heer, 1838:39 (*ex parte*). Schiødte, 1841:356. Küster, 1846:7; Letzner, 1849:50. LeConte, 1850:209. 1853:401, 402. Fairmaire and Laboulbène, 1854:6. Lacordaire, 1854:44 (*ex parte*). Schaum, 1856:68. Jacquelin du Val, 1857:6. Thomson, 1859:3, 192. LeConte, 1861:7. Stierlin, 1869:10. Crotch, 1873:4. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Schaupp, 1878:6. Marseul, 1880:29. Horn, 1881:111. Bedel, 1881:22. Fauvel, 1882:81. LeConte and Horn, 1883:10. Marseul, 1882:4. Seidlitz, 1891:4, 19. Ganglbauer, 1892:122. Semenov, 1895:305. Everts, 1898:48. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:104. Blatchley, 1910:48. Kuhn, 1912:31, 50. Fairmaire, 1913:30. Schaufuss, 1916:28, 29. Porta, 1923:78. Semenov, 1926:39. Portevin, 1929:40. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:216. Hatch, 1953:63. Lindroth, 1954:3. Antoine, 1955:47. Ball, 1960:108. Nakane *et al.*, 1963:19. Ohkura, 1973:4. Lindroth, 1974:32.

### Adults

*Diagnostic combination.*— Distinguished from other elaphrines by large eyes, by lack of striae on elytra (in some species suggested at base), and by presence of setigerous punctures on intervals 3, 5, 7 and 9.

*Description.*— Medium-sized: 6 to 10 mm.

*Head.* Eye large, medial margin of eye higher than frons. Fronto-ocular sulcus indistinct (Fig. 16). Clypeus without impression. Apical retinacular tooth of right mandible single or double, and its basal terebral tooth prominent (Figs. 3 and 4). Maxillary palpomere 3, 0.3 to 0.5 as long as palpomere 4 (Fig. 7). Mentum (Fig. 10) with one pair of setae.

*Thorax.* Pronotum with lateral margin not explanate, and with one seta or without seta. Scutellum without transverse ridge basally. Postero-lateral ridge of mesosternum weakly developed or absent. Postero-lateral setae of metanotum small to very small.

*Abdomen.* Tergum 2 with one pair of submedial ridges posteriorly. Tergum 1 without setae. Abdominal sternum 7 with one or two pairs of setae on posterior margin.

*Elytron.* Striae barely traceable at base or absent. (Figs. 31, 110 to 117); intervals not clearly delineated, but intervals 3, 5, 7 and 9 outlined by alternation of crater-like impressions (pits) and brilliant surface (mirror). Pits delimited externally by punctures in semicircular stria, by depressions between intervals, by contrasting color (golden-copper band), or by elongate punctures; base of elytron with two pits lacking setigerous punctures on intervals 5 and 7; scutellar setigerous punctures elevated, but not situated in circular pit. Mirrors (when present) situated between two pits of same interval; each elytron with one to 20 mirrors. Surface with four rows of pits bearing central setigerous puncture in intervals 3, 5, 7 and 9; interval 3 with five or six setigerous punctures, interval 5 with four, interval 7 with four, and interval 9 with seven or eight. Setigerous punctures large (40 to 50 microns, smaller in *E. lapponicus*), antero-medially emarginate and elevated. Punctures present over elytra except on mirrors.

*Wings.* Venation similar to that of species of other genera except for subangular posterior end of oblongum (Fig. 32).

*Legs.* Foreleg: trochanter with one, two or three setae, femur (Figs. 145 and 146) with 30 setae or more, fringe on medio-dorsal surface of tibia on apical 0.5 to 0.8. Midleg: coxa with numerous setae, trochanter with one, two or three setae, femur (Figs. 147 and 148) with 27 setae or more. Hindleg: coxa with three to 40 setae.

*Male genitalia.* Baso-lateral and ventral surface of median lobe strongly sclerotized, and sharply delineated from weakly sclerotized dorsal surface (Fig. 40a). Stylet of internal sac large, protruded well beyond basal orifice, and spatulate anteriorly.

*Ovipositor.* Basal sclerite of stylus with lateral and medial ridges dorsally, with small setae on dorsal ridges, and with or without setae apically. Apical sclerite of stylus with two to six very small stout setae along dorsal ridges, apex without or with one or two very small setae (Figs. 72 to 75).

### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other elaphrine genera by barely suggested lacinia, and by enlarged basal inner margin of mandible (therefore, basal margin not directly in line with apical one).

### First Instar Larvae

*Description.*— Ultimate length 6 to 7 mm. Medial portion of nasale subacutely or acutely pointed, teeth absent or present; teeth very fine, fine or medium-sized, and lacking medially (Figs. 89b to 92b). Angle formed by setae DI-A, and pores DI-P and DMP-E 130° or less. Base of mandible enlarged, and basal inner margin not in line with apical inner margin (Figs. 80 and 81). Lacinia barely suggested (Fig. 85c); seta apical and small. Ventral surface of stipes with membranous declivity behind postero-lateral seta, or completely sclerotized. Microsculpture of urogomphus single-pointed or lacking.

### Second Instar Larvae

*Description.*— Ultimate length 7 to 9 mm. Accessory setae absent from ventral surface of stipes. Each sclerite of pronotum and mesonotum respectively with 15 to 45 and with 8 to 40 accessory setae. Abdominal epipleuron of segments 1 to 8 entire.

### Third Instar Larvae

*Description.*— Ultimate length 11 to 15 mm. Each sclerite of mesonotum with 25 to 100 accessory setae.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— Species of this Holarctic genus live in arctic, boreal and temperate regions, from the British Isles to Kamchatka, and from Alaska to Newfoundland.

### Key to subgenera of *Elaphrus* Fabricius

#### Adults

- 1 Fringe of setae on posterior margin of pronotum extended to posterior angle (Figs. 20 to 25). Suture between proepisternum and proepimeron not evident. Males with first three tarsomeres slightly expanded and with

- spongy pubescence ventrally, or not expanded and without spongy pubescence ..... 2
- 1' Fringe of setae on posterior margin of pronotum not reaching posterior angle (Figs. 17 to 19). Suture between proepisternum and proepimeron evident. Males with first four tarsomeres slightly expanded and with spongy pubescence ventrally ..... 3
- 2 (1) Clypeus with four to six setigerous punctures. Disc of prosternum and process of mesosternum with setae. Trochanter of foreleg and midleg with three setigerous punctures. Coxa of hindleg with setae covering surface ..... *Elaphrus* Fabricius p. 282
- 2' Clypeus with two setigerous punctures. Disc of prosternum and process of mesosternum asetose. Trochanter of foreleg with two, that of midleg with one or two setigerous punctures. Coxa of hindleg with setae restricted to mesial half of surface. .... *Elaphroterus* Semenov p. 322
- 3 (1') Maxillary palpomere 3, 0.5 as long as palpomere 4. Disc of prosternum and lateral portion of metasternum setose. Elytral pits with one to six irregularly arranged punctures (Fig. 131). Microsculpture on elytra strongly convex and widespread ..... *Arctelaphrus* Semenov p. 241
- 3' Maxillary palpomere 3, 0.3 as long as palpomere 4. Disc of prosternum and lateral portion of metasternum asetose. Elytral pits with at least eight regularly distributed punctures (Figs. 132 to 136). Microsculpture on elytra at most convex and not covering entire surface ..... *Neolaphrus* Hatch p. 246

### All instar larvae

- 1 Head elongate: bisinuation of lateral margin behind eye with anterior convexity longer than posterior one (Figs. 89a and 90a). Epicranial suture at least 0.7 as long as antennal scape. Medial point of nasale obtused (Figs. 89b to 90b). Maxillary palpomere 1, 1.5 (first and second instar larvae) or 1.2 (third instar larvae) as long as palpomere 2. Baso-ventral pores of stipes distant: submedial pore situated distinctly anterior to sublateral one (Fig. 85b) ..... 2
- 1' Head short: bisinuation of lateral margin behind eye with anterior and posterior convexities subequal (Figs. 91a and 92a). Epicranial suture no more than 0.6 as long as antennal scape. Medial point of nasale acute (91b and 92b). Maxillary palpomere 1, 1.0 (first instar larva), or 0.8 (second instar larva), or 0.7 (third instar larva) as long as palpomere 2. Baso-ventral pores of stipes adjacent: submedial pore slightly anterior to external one (Fig. 83b) ..... 3
- 2 (1) Ventral surface of stipes with membranous embayment behind posterolateral seta (Fig. 83b). Mesonotal and metanotal seta PII-P very small; anterior seta of outer poststernite of segment 9 very small ..... *Arctelaphrus* Semenov p. 241
- 2' Ventral surface of stipes entirely sclerotized (Fig. 85b). Mesonotal and metanotal seta PII-P small; anterior seta of outer poststernite of segment 9

- medium-sized ..... *Neoelaphrus* Hatch p. 246
- 3 (1') Teeth of nasale absent or fine (Fig. 91b). Posterior band of mesonotum and metanotum with pointed sculpture on 0.3 of its surface. Inner seta of inner poststernite on segments 1 to 9 very small ..... *Elaphrus* Fabricius p. 282
- 4' Teeth of nasale present and slightly coarser than in larvae of subgenus *Elaphrus* (Fig. 92b). Posterior band of mesonotum and metanotum with pointed sculpture on 0.5 or more of its surface. Inner seta of inner poststernite on segment 1 to 8 small, that on segment 9 clearly larger .....  
..... *Elaphroterus* Semenov p. 322

### Subgenus *Arctelaphrus* Semenov

*Arctelaphrus* Semenov, 1926:39. Type-species: *Elaphrus lapponicus* Gyllenhal, 1810, fixed by Semenov (1926), by original designation. Ball, 1960:106. Lindroth, 1961:111.

*Elaphrus* Semenov, 1895:309. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:104. Bänninger, 1919:149. *Ex Parte*.

### Adults

**Diagnostic combination.**— Distinguished from adults of other subgenera as in following. Disc of prosternum setose. Suture between proepisternum and proepimeron sharply delineated. Setigerous punctures in intervals 3, 5 and 7 small (25 microns in diameter), others large (40 to 50 microns in diameter). Elytral pits (Fig. 31) with a few irregularly arranged punctures.

**Description.**— *Head.* Frons without medial fovea. Clypeus with one pair of setae. Terebral margin of right mandible 0.3 as long as mandible (Fig. 3); basal retinacular tooth emarginate; apex of retinacular tooth situated anterior of terebral tooth. Maxillary palpomere 3, 0.5 as long as palpomere 4. Galeomere 1 subequal to maxillary palpomere 2.

*Thorax.* Lateral margin of pronotum completely beaded. Fringe of setae on posterior margin not extended to hind angles; setae of fringe scimitar-shaped and narrow. Suture between proepisternum and proepimeron sharply delineated. Disc and apophysis of prosternum setose. Process of mesosternum asetose; postero-lateral ridge of mesosternum outlined.

*Abdomen.* Tergum 7 without setae.

*Elytron.* Striae indistinct at base (Fig. 110). Transverse basal stria sharply outlined at shoulder. Setigerous punctures of intervals 3, 5 and 7, 25 microns in diameter, those of interval 9 and scutellar interval 40 to 50 microns in diameter. Mirrors of interval 3 subequal in width. Elytral pits with few irregularly arranged punctures (Fig. 131).

*Legs.* Foreleg: trochanter with two setae; femur with about 70 setae; tibia with about 34 setae; inner dorsal fringe of tibia 0.5 as long as tibia, and with about eight setae posteriorly; first four tarsomeres of males with spongy pubescence ventrally. Midleg: coxa with few accessory setae; trochanter with one or two setae; femur with about 75 setae; tibia with about 80 setae. Hindleg: coxa with about 10 setae on inner 0.5 of process; femur with about 20 setae; tibia with about 125 setae.

*Male genitalia.* Internal sac of median lobe with large scales posteriorly.

*Ovipositor.* Basal sclerite of stylus with some very small setae ventrally; apical sclerite with few stout setae on dorso-lateral and dorso-medial ridges, and apex with two very small setae (Fig. 72).

### All Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of other subgenera as in following. Epicranial suture as long as or longer than antennal scape (Fig. 89a). Ventral surface of stipes with membranous declivity behind posterior seta, and with two posterior pores distant (Fig. 85b).

### First Instar Larvae

**Description.**— Medial point of nasale obtuse; teeth of nasale large and terminated subapically on medial point (Fig. 89b). Epicranial suture subequal to or longer than antennal scape (Fig. 89a). Head elongate: bisinuation behind eye with anterior convexity longer than posterior one. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 110° to 130°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale equilateral. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin asetose; dorsal surface with about 30 setae on inner 0.5, subapical setae roughly distributed in one row; two postero-ventral pores distant (Fig. 85b).

## Second Instar Larvae

Not seen, but briefly described by Luff (1976); similar to third instar larvae except for smaller head (width 0.8 mm). I assume this instar can be recognized, as in nearly all species of *Elaphrus*, by smaller projections on urogomphus (largest one about 0.5 size of that of third instar).

## Third Instar Larvae

**Description.**— Prementum with less than two setae dorso-laterally. Proepisternum with 15 accessory setae. Largest projection of urogomphus in lateral view medium-size (Fig. 97). Each sclerite of terga 1 to 8 with about 37 accessory setae. Hypopleuron of abdominal segments 1 to 8 each with 19 accessory setae. Sternite of abdominal segment 1 with two accessory setae, those of segments 2 to 7 each with about 22, those of segments 8, 9 and 10 respectively with 30, nine and eight.

## Geographical Distribution and Affinities, and Notes

**Distribution.**— The Holarctic range of the only species of this subgenus is restricted to subarctic regions.

### *Elaphrus lapponicus* Gyllenhal

**Diagnostic combination.**— Setigerous punctures on intervals 3, 5 and 7 small (25 microns in diameter). Elytron with very convex microsculpture; pits clearly outlined by punctures, each with few irregular punctures (Figs. 118 and 131).

### *Elaphrus lapponicus lapponicus* Gyllenhal new status

Figs. 3a-b, 7, 10, 16, 31, 72, 89a-b, 97, 110, 157

*Elaphrus lapponicus* Gyllenhal, 1810:8. Type locality: Lappland, subsequently restricted to Abisko, Sweden, (Lindroth 1961); type in Göteborg Museum; seen by Lindroth (1961). Dejean, 1826:73. Gyllenhal, 1827:397. Schaum, 1856:70. Seidlitz, 1875:2. Marseul, 1882:4. Semenov, 1895:310. Jacobson, 1906:267. Joy, 1932:328. Lindroth, 1961:111. 1974:32.

*Elaphrus elongatus* Fischer von Waldheim, 1828:266. Type locality: Kamchatka, USSR; type in Zoological Museum, University, Helsinki; seen by Lindroth (1961). Marseul, 1882:4. Lindroth, 1961:111.

*Elaphrus elongatus*; Semenov, 1895:310.

*Elaphrus obscurior* Kirby, 1837:63. Type locality: Latitude 65°— according to Lindroth (1961) near Great Bear Lake, N.W.T.; type in British Museum of Natural History, London; type seen by Lindroth (1961). Crotch, 1876:246. Schaupp, 1878:6. Marseul, 1882:4. Lindroth, 1961:111.

*Elaphrus lapponicus* var. *elongatus*; Jacobson, 1906:267.

## Adults

**Diagnostic combination.**— Distinguished from adults of *E. lapponicus obliteratus* by smaller size (elytral length (EL) of most specimens less than 5.4 mm).

**Description.**— Dorsal body surface black to brilliant green and copper. Elytral pits generally not clearly delineated. Frontal impression of head indistinct or clearly delineated. Pronotum with one pair of discal impressions. Elytral pits barely or clearly impressed; lateral ridges in pits either absent, suggested, or clearly delineated. Head wide and pronotum long (means of the following ratios were significantly different from those of *E. lapponicus obliteratus*: PW/HW less than 1.05, EL/HW less than 2.32, EW/HW less than 0.830, and PL/EL more than 0.39).

**Integument sculpture.** Puncture 20 microns in diameter on scutellum and all coxae, 25 to 30 microns in diameter on dorsal body surface and on thoracic sterna, and 30 to 40 microns in diameter on pleura and on lateral portion of abdominal sterna. Punctures 25 to 50 microns apart generally, but sparser on scutellum, elytron, medial portion of thoracic sterna, and coxae.

Microsculpture absent from or indistinctly outlined on scutellum and on base of mesosternum, convex on abdominal sterna, on elytron, and on metepisternum, and flat on remaining sclerites.



Table 1. Descriptive statistics for *E. lapponicus lapponicus*, based on 10 males and 10 females from mainland northwestern North America (Alaska, Yukon, North West Territories, Alberta, and British Columbia).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.65–1.97	1.85	0.140	0.043	5.0
PW	1.85–2.22	2.08	0.165	0.049	5.3
EL	4.20–5.10	4.68	0.375	0.113	5.4
HW	1.87–2.15	2.05	0.109	0.032	3.5
B. Proportions					
PL/PW	0.830–0.927	0.886	0.043	0.013	3.2
PL/EL	0.366–0.418	0.395	0.019	0.006	3.1
PL/EW	1.030–1.190	1.110	0.052	0.015	3.1
PL/HW	0.825–0.938	0.902	0.044	0.013	3.2
PW/EL	0.425–0.468	0.446	0.020	0.006	3.1
PW/EW	1.190–1.330	1.260	0.063	0.019	3.3
PW/HW	0.925–1.070	1.020	0.052	0.015	3.4
EL/EW	2.720–3.000	2.820	0.101	0.030	2.4
EL/HW	2.150–2.380	2.290	0.105	0.031	3.1
EW/HW	0.725–0.852	0.810	0.049	0.015	4.0

*Male genitalia.* Apex of median lobe in dorsal view with sharp point on right side near base of apical spatula (Fig. 40b), in lateral view spatula moderately expanded and slightly bent ventrally; both right and left paramere wide with short setae extended in apical 0.3 (Figs. 40c, 40d); internal sac as in Fig. 40a.

*Measurements and proportions.*— See Table 1.

*Variation.*— Two composite samples, one from Scandinavia and one from Alaska, were studied. In Scandinavia, adults are generally larger, the elytral sculpture is little impressed and the pronotum is relatively wide (mean of ratio PW/EL is significantly larger than means of the mainland North American sample). In North America the pronotum is relatively long (mean of ratio PL/PW is significantly larger than that of Scandinavian sample).

### Third Instar Larvae

*Diagnostic combination.*— Head, pronotum and most of tergum (including base of urogomphi) orange.

*Description.*— Head (except for darker area near frontale), disc of pronotum and mesonotum, and most of tergum 9 including base of urogomphi orange; remainder dark brown and dull (preserved specimens tend to fade to brown). Prementum with less than three accessory setae dorso-laterally. Meshed microsculpture present on entire dorsal surface and latero-ventral surface of parietale, and on all of nota.

*Note about description.*— Luff (1976) described briefly the first and second instar larvae. I did not have access to these. I studied only a third instar larva collected by Lindroth. This specimen was very pale, thus for color I used descriptions by Lindroth (1954) and Luff (1976).

### Geographical Distribution and Affinities, and Notes

*Distribution.*— This Holarctic subspecies lives in the subarctic regions, from northern British Isles to Kamchatka (Lindroth, 1945), and from Alaska to Labrador. For North American distribution see Fig. 157.

*Collecting notes.*— Adults are hygrophilous, and live near cold waters. The preferred substrate is of neutral PH where mosses of the genus *Paludella* and other short vegetation such as *Marchantia* grow. Exposure is sunny, though some small and scattered conifers are present in some sites. This type of habitat is found near springs, brooks and small ponds. Adults are mostly seen in spring, but occur sporadically also later in summer. Fully grown third instar larvae and teneral adults were collected in July in Labrador, thus adults probably overwinter. Adults probably fly as suggested by two specimens collected on the shore of Lesser Slave Lake, Alberta, in an atypical habitat.

*Taxonomic notes.*— See discussion under *E. lapponicus obliteratus*. I studied 80 adults and one third instar larva.

#### *Elaphrus lapponicus obliteratus* Mannerheim new status Figs. 40a-d, 118, 131, 157

*Elaphrus obliteratus* Mannerheim, 1853:117. Type locality: Paul Harbour, Kodiak Island, Alaska; type in Zoological Museum, University, Helsinki; type seen by Lindroth (1961). Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Marseul, 1882:4. Lindroth, 1961:111.

### Adults

*Diagnostic combination.*— Distinguished from adults of *E. lapponicus lapponicus* by their large size (elytral length (EL) mostly more than 5.5 mm).

*Description.*— As in *E. lapponicus lapponicus* except as follows. Head narrow and pronotum short (means of the following ratios were significantly different from those of *E. lapponicus lapponicus*: PW/HW greater than 1.058, EL/HW more than 2.36, EW/HW more than 0.846 and PL/EL less than 0.386).

*Variation.*— See Table 2 and discussion under *E. lapponicus lapponicus*.

*Distribution.*— Known from a few localities in the United States. ALASKA: Kodiak Island: Bare Lake (10; UASM, MCZC), Pinguicula Lake (12; UASM, MCZC), R.A. (Russian America) (1; BMNH).

*Collecting notes.*— Lindroth (1969b) and Ball (pers. comm.) reported specimens of this subspecies as abundant in sphagnum bogs.

*Taxonomic notes.*— Adults of many species of ground beetles are larger and brighter in regions with cool or cold maritime climate than elsewhere (Lindroth, 1955 and 1961). Adults of *E. lapponicus* are also larger in these regions (Norway, coastal mainland Alaska, Labrador and Kodiak). However, those from Kodiak are much larger than expected. My interest in them arose when G.E. Ball noted that he collected them on sphagnum moss, which is a habitat avoided by the mainland specimens.

I also studied ratios derived from measurements. Both samples from Scandinavia and western North America differ significantly from those of Kodiak in means of six ratios. These ratios were tested in relation to body size for correlation. Within each sample, there seems to be little or no correlation with size. However, there is a weak correlation with size between samples for ratios PW/HW and EW/HW. Mainland specimens differ significantly from the Kodiak sample in means of two ratios PL/EL and EL/HW. The Norway sample is significantly different from the Kodiak sample in the mean of ratio PW/EL, and from mainland North American sample in the mean of ratio PL/PW. Scandinavian and North American sample differ significantly from each other in the mean of ratios PW/EL and PL/PW.

Table 2. Descriptive statistics for *E. l. obliteratus*, based on 12 males and eight females from Pingicula Lake and Bare Lake, both localities on Kodiak Island, Alaska.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.00–2.32	2.20	0.121	0.036	3.7
PW	2.40–2.72	2.56	0.125	0.037	3.2
EL	5.15–6.20	5.75	0.359	0.107	4.2
EW	1.90–2.20	2.04	0.133	0.038	4.3
HW	2.25–2.52	2.39	0.105	0.031	2.9
B. Proportions					
PL/PW	0.818–0.880	0.857	0.026	0.008	2.0
PL/EL	0.364–0.395	0.382	0.013	0.004	2.3
PL/EW	1.040–1.130	1.070	0.040	0.012	2.5
PL/HW	0.874–0.968	0.918	0.034	0.010	2.5
PW/EL	0.421–0.471	0.446	0.019	0.006	2.8
PW/EW	1.200–1.320	1.250	0.051	0.015	2.7
PW/HW	1.030–1.130	1.070	0.041	0.012	2.5
EL/EW	2.680–2.950	2.810	0.114	0.034	2.7
EL/HW	2.280–2.550	2.400	0.117	0.035	3.3
EW/HW	0.809–0.903	0.857	0.037	0.011	2.9

As observed in many other carabid species common to both regions, slight differences between North American and Scandinavian populations are expected. Despite the great geographical gap between both samples, they are essentially the same, except for the narrower pronotum in specimens from North America. However, differences between above samples and that of Kodiak suggest lack of gene flow over a long period, and the independant evolution of the Kodiak population. Habitat differences, significant difference in means of ratios PL/EL and EL/HW, and large size (taxonomically significant) justify ranking the allopatric Kodiak population as a distinct subspecies.

Lindroth (1969b: 195–210) in his account of the Kodiak carabid fauna found no evidence of endemic species or races. However, he felt that some carabid species existed in this refugium during at least the last glaciation because of the higher proportion of micropterous species than on nearby coastal regions of Alaska. A postglacial recolonization, he assumed, would have produced a higher proportion of macropterous individuals. Ball (1969) studied six micropterous species of *Pterostichus* in the subgenus *Cryobius*. He found that three were not different from nearby Kenai Peninsula. Of remaining species, *P. parasimilis* Ball differed slightly in color, and *P. pinguedineus* Eschscholtz and *P. riparius* Dejean showed longer elytra (means for each sex were significantly different) than those of populations from other coastal Alaskan localities. However, he found no differences in ratios or in behaviour. Moreover, Smetana (1971) described the Kodiak population of the staphylinid *Quedius labradorensis* Smetana, characterized by longer size and relatively wider pronotum, as an endemic subspecies *Q. labradorensis insularis*. Thus, there is evidence for the existence of a refugium on Kodiak Island during the last glacial period as shown by structural differences in adults of some species

of beetles occurring both on the island and on the mainland. Since specimens of *E. lapponicus* tolerate cold, I feel that these beetles survived in the refugium through one or more glacial periods when selection was probably intensive.

### Subgenus *Neolaphrus* Hatch

*Neolaphrus* Hatch, 1951:113. Type-species: *Elaphrus uliginosus* Fabricius, 1792, fixed by Hatch (1951), by original designation. Hatch, 1953:63. Ball, 1960:106. Lindroth, 1961:112. Nakane, et al. 1963:18.

*Elaphrus*: Semenov, 1895:309 (*ex parte*). Jacobson, 1906:267 (*ex parte*). Reitter, 1908:96, 97 (*ex parte*). 1909:104 (*ex parte*). Bänninger, 1919:149 (*ex parte*). Porta, 1923:78. Semenov, 1926:39. Portevin, 1929:41. Jeannel, 1941:216.

### Adults

**Diagnostic combination.**— Distinguished from adults of other subgenera as in following. Hind coxa and hind femur respectively with less than six setae. Prosternum without setae on disc. Suture between proepisternum and proepimeron sharply delineated.

**Description.**— *Head.* Frons with medial fovea, in some species with additional smaller foveae posteriorly. Clypeus with one pair of setae. Terebral margin of right mandible less than 0.5 as long as mandible; basal retinacular tooth emarginate; apex of retinacular tooth situated anteriorly of terebral tooth. Maxillary palpomere 3, 0.3 to 0.4 as long as palpomere 4. Galeomere 1, 1.5 as long as maxillary palpomere 2.

*Thorax.* Lateral margin of pronotum completely beaded or unbeaded. Fringe of setae on posterior margin of pronotum ended before hind angles; setae scimitar-shaped and narrow. Suture between proepisternum and proepimeron sharply delineated. Prosternum asetose on disc, but setose on process. Process of mesosternum asetose; postero-lateral ridge of mesosternum absent or weakly outlined.

*Abdomen.* Tergum 7 with setae along anterior margin or on entire surface.

*Elytra.* Striae lacking or suggested at base. Transverse basal stria sharply outlined at shoulder. Setigerous punctures of elytron 40 to 50 microns in diameter. Mirrors of similar width in interval 3. Elytral pits with fewer than 30 irregularly distributed punctures (Figs. 132 to 134).

*Legs.* Foreleg: trochanter with one or two setae; femur with 32 to 57 setae; tibia with 19 to 25 setae; inner dorsal fringe 0.6 as long as tibia, and without setae posteriorly; first four tarsomeres of males with ventral spongy pubescence. Midleg: trochanter with one or two setae; femur with 27 to 58 setae; tibia with 56 to 80 setae. Hindleg: coxa with three to six setae on inner half of process; femur with five to 11 setae; tibia with 51 to 80 setae.

*Male genitalia.* Internal sac of median lobe with large scales posteriorly.

*Ovipositor.* Basal sclerite of stylus with numerous very small setae apico-ventrally; apical sclerite with few stout setae on dorso-lateral and dorso-medial ridges, apex of sclerite with one very small seta or in some species with one more extremely small seta (Fig. 73).

### All Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of other subgenera as in following. Epicranial suture 0.8 to 1.2 as long as scape (Fig. 90a). Ventral surface of stipes thickly sclerotized, and two posterior pores distant (Fig. 85b).

### First Instar Larvae

**Description.**— Medial point of nasale obtuse; teeth of nasale absent or large and ending subapically on medial point (Fig. 90b). Epicranial suture 0.8 to 1.2 as long as antennal scape. Head elongate: bisinuation of lateral margin behind eye with anterior convexity longer than posterior one (Fig. 90a). Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 110 to 130°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale equilateral. Stipes entirely sclerotized ventrally; lateral margin entire; dorsal surface with about 30 setae on inner half, subapical setae roughly distributed in one row; two postero-ventral pores distant (Fig. 85b).

### Second Instar Larvae

**Description.**— Outer margin of stipes entire. Each sclerite of mesonotum with about 15 accessory setae. Each sclerite of terga 1 to 8 with 16 to 36 accessory setae. Basal major accessory setae on urogomphus postero-lateral; microsculpture on urogomphus barely suggested or scale-like. Pointed microsculpture absent from anterior band of terga 1

to 8, present on (10% of surface) or absent from anterior band of tergum 9, and present on (5% of surface) or absent from posterior band. Hypopleuron of abdominal segments 1 to 8 with eight to 20 accessory setae.

### Third Instar Larvae

**Description.**— Prementum with about six accessory setae dorso-laterally. Proepisternum with 25 accessory setae. Large projection of urogomphus in lateral view medium-sized or large (Figs. 98c, 99b). Each sclerite of terga 1 to 8 with 35 to 140 accessory setae. Epipleuron of abdominal segments 2 to 8 with 17 to 60 accessory setae. Hypopleuron of abdominal segments 1 to 8 each with 14 to 47 accessory setae. Sternite of abdominal segment 1 with four to 12 accessory setae, those of segments 2 to 7 each with 18 to 24, that of segment 8 with 18 to 38, that of segment 9 with two to eight, and that of segment 10 with six to 12.

### Geographical Distribution and Affinities, and Notes

**Distribution.**— The ranges of species of this subgenus extend across Palaearctic and Nearctic regions, from the subarctic to the temperate zones.

**Taxonomic notes.**— Species of this subgenus are arranged in three species groups: the *uliginosus* group, the *fuliginosus* group and the *cupreus* group. Each group is characterized in the key as well as in the text. My main reasons for giving formal recognition to these three monophyletic groups were zoogeographical. The *uliginosus* group is restricted to the Palaearctic region, the *fuliginosus* group is restricted to the eastern Nearctic region, and the *cupreus* group has two lineages of which one is Palaearctic and the other Nearctic.

### Key to species of subgenus *Neoelaphrus* Hatch

#### Adults

- 1 Fringe of setae on posterior margin of pronotum ending 40 to 120 microns from postero-lateral angles (Fig. 17a). Lateral margin of pronotum in lateral view sinuate near middle, pronotal epipleuron narrowest at this point (Fig. 17b). Bead of pronotal lateral margin 20 to 30 microns in width. Pronotum with one antero-submedial impression (indistinct in individuals of *E. splendidus*). Palaearctic Region ..... 2
- 1' Fringe of setae on posterior margin of pronotum ending 150 to 250 microns from postero-lateral angles (Figs. 18a and 19). Lateral margin of pronotum in lateral view not sinuate near middle, pronotal epipleuron equally narrow from middle to anterior margin (Fig. 18b). Bead of pronotal lateral margin either absent, 10 to 15 microns in width, or 20 to 30 microns in width. Pronotum without antero-submedial impression ..... 6
- 2 (1) Elytron with four rows of sharply outlined and subconvex mirrors on intervals 3, 5, 7 and 9. Upper surface of body including elytral pits brilliant metallic golden green. Pronotum without or with suggested antero-submedial impressions on each side. Punctures 30 to 40 microns in diameter, on elytral intervals 4, 6 and 8, and 20 to 25 microns in diameter on head and pronotum. Eastern Siberia .....  
..... *E. splendidus* Fisher von Waldheim p. 254
- 2' Elytron with one or two rows of sharply outlined and flat mirrors on intervals 3, or 3 and 5. Upper surface of body not brilliant green, (except in *E. pyrenaeus*); elytral pits purple, or if green, then elytral surface brown-copper. Pronotum with clearly defined antero-submedial

- impressions. Punctures 20 to 25 microns in diameter on head, pronotum and elytral intervals, 4, 6 and 8 ..... 3
- 3 (2') Punctures 100 to 150 microns apart on intervals 4, 6 and 8. Lateral ridges of elytral pits convex and wide (Fig. 132). Northern Japan and adjacent regions of USSR ..... *E. japonicus* Uéno p. 254
- 3' Punctures 30 to 40 microns apart on intervals 4, 6 and 8. Lateral ridges of elytral pits weakly convex, narrow or absent (Figs. 119 and 120) ..... 4
- 4 (3') Dorsal surface of body bright brown-copper. Elytral pits metallic green. Kansu, China ..... *E. potanini* Semenov p. 259
- 4' Dorsal surface of body dark, or brilliant green or brilliant brown-copper in few specimens. Elytral pits purple ..... 5
- 5 (4') Dorsal surface of body dark green or copper (some individuals brilliant). Intervals 4, 6 and 8 subcostate (except specimens from central Asia). Meshes of microsculpture clearly outlined on elytron (Fig. 137). Elytral pits slightly impressed (Fig. 119). Europe east to Yenisey River and western China ..... *E. uliginosus* Fabricius p. 255
- 5' Dorsal surface of body brilliant green-olive or brown-copper. Intervals 4, 6 and 8 not costate. Meshes of microsculpture absent from elytron except near shoulder, elytral pits and postero-lateral impressions of pronotum (Fig. 138). Elytral pits deeply impressed (Fig. 120). Southern Spain to Pyrénées ..... *E. pyrenoeus* Motschulsky p. 258
- 6 (1') Lateral margin of pronotum unbeaded or beaded; bead, when present, 20 to 30 microns in width. Punctures of pleura and lateral portion of abdominal sterna 30 to 45 microns in diameter; punctures apparently larger (about 80 microns in diameter) because of widely depressed area around each puncture—best seen on proepisternum (Fig. 107). Abdominal sterna 5 and 6 each with fewer than three accessory setae medially (Fig. 139). Tibia of foreleg of male with large projection at base of posterior spur and with small projection at base of apical spur—best seen in posterior view (Fig. 149). Eastern Nearctic Region ..... 7
- 6' Lateral margin of pronotum beaded, bead 10 to 15 microns in width. Punctures of pleura and lateral portion of abdominal sterna 20 to 35 microns; area around each puncture narrowly or not depressed (Fig. 108). Abdominal sterna 5 and 6 each with five to 15 accessory setae, or accessory setae lacking then punctures of ventral body surface 20 to 25 microns apart. Tibia of foreleg of male without projection at base of both spurs (cuticle at base of posterior spur in some specimens sharp but not projected ..... 9
- 7 (6) Dorsal body surface dark green. Lateral margin of pronotum beaded; bead 20 to 30 microns in width. Dorsal surface of tibia and tarsomeres metallic green. Abdominal sternum 7 of males with 10 to 20 accessory setae ..... *E. fuliginosus* Say p. 260
- 7' Dorsal body surface dark copper or brass-silver. Lateral margin of pronotum not beaded (Fig. 107). Dorsal surface of tibia and tarsomeres metallic purple. Abdominal sternum 7 of males without accessory setae (Fig. 139) ..... 8

- 8 (7') Dorsal body surface nearly black with copper hue. Antennomeres 1 to 3 black. Lateral ridges of elytral pits convex and wide (Fig. 132). Elytral mirrors present on intervals 3 and 5; mirrors little contrasted against dark background color of intervals 2, 4 and 6. Trochanter of foreleg with one seta (Fig. 145). Punctures of dorsal body surface 10 to 200 microns apart  
..... *E. cicatricosus* LeConte p. 262
- 8' Dorsal body surface brass-silver. Antennomeres 1 to 3 reddish brown. Lateral ridges of elytral pits suggested or absent (Fig. 121). Elytral mirrors present on interval 3 only; mirrors sharply contrasted against silver background of intervals 2 and 4. Trochanter of foreleg with two setae. Punctures of dorsal body surface 10 to 30 microns apart on head and on elytral intervals 4, 6 and 8, and 20 to 40 microns on pronotum (Figs. 104 and 121) ..... *E. lindrothi* new species p. 264
- 9 (6') Lateral ridges of elytral pits wide and not fused anteriorly or posteriorly (Fig. 132). Elytral mirrors contrasting against duller intervals 2, 4 and 6. Microsculpture flat or subconvex on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 132). Palaearctic Region ..... 10
- 9' Lateral ridges of elytral pits distinctly fused anteriorly and posteriorly or indistinctly so (then ridges narrow) (Figs. 133 and 134). Elytral mirrors weakly contrasted against brilliant intervals 2, 4, 6 and 8. Microsculpture absent or suggested in spots on head, pronotum and intervals 4, 6 and 8 (Figs. 133 and 134). Nearctic Region ..... 11
- 10 (9) Tarsomeres and apex of tibiae metallic green dorsally; dorsal body surface greenish with bright green pronotal and head impressions. Punctures of dorsal body surface dense: punctures three to ten microns apart and polygonal near anterior angles of frons at level of clypeal setae, 30 to 50 microns apart on disc of pronotum and elytral intervals 4, 6 and 8, and space between suture and first pit of interval 3 with three to four rows of punctures; punctures 25 to 30 microns in diameter on clypeus, and 25 to 35 microns in diameter near antero-lateral angles of frons. Eastern Palaearctic Region ..... *E. sibiricus* Motschulsky p. 266
- 10' Tarsomeres and apex of tibiae purple; dorsal body surface dark copper with blue-green pronotal and head impressions. Punctures of dorsal body surface sparse: punctures 10 to 30 microns apart and round near anterior angles of frons at level of clypeal setae, 50 to 100 microns apart on disc of pronotum and elytral intervals 4, 6 and 8, and space between suture and first pit of interval 3 with one or two rows of punctures; punctures 15 to 20 microns in diameter on clypeus and near antero-lateral angles of frons. Palaearctic Region ..... *E. cupreus* Duftschmid p. 268
- 11 (9') Punctures 10 to 100 microns apart on pleura and laterally on basal abdominal sterna. Male tibia of midleg with sharp projection at base of inner spur (Fig. 150). Punctures of elytral intervals 4, 6 and 8, 30 to 120 microns apart (Fig. 122) ..... *E. clairvillei* Kirby p. 271
- 11' Punctures 10 to 20 microns apart on pleura, and laterally on basal abdominal sterna. Male tibia of midleg without projection at base of inner spur. Punctures of elytral intervals 4, 6 and 8, either 10 to 20 microns

- apart, or more than 200 microns apart ..... 12
- 12 (11') Dorsal body surface olive, blue-green, dark brown-olive, or red-brown; dorsal surface of tibia and tarsomeres metallic green or copper; antennomeres 1 to 3 brown. Pronotum with two submedial impressions. Lateral ridges of elytral pits narrow and weakly convex (Fig. 134). Punctures 15 to 20 microns apart on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123). Abdominal sterna 5, 6 and 7 each without or with fewer than three accessory setae. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276
- 12' Dorsal body surface brilliant black; dorsal surface of tibia and tarsomeres metallic purple; antennomeres 1 to 3 black. Pronotum with one submedial impression. Lateral ridges of elytral pits wide and convex (Fig. 133). Punctures about 60 microns apart on head, 10 to 200 microns apart on pronotum and 200 microns apart on elytra. Abdominal sterna 5, 6 and 7 with five to 20 accessory setae. California to westernmost Nevada ..... *E. laevigatus* LeConte p. 280

#### First Instar Larvae

- 1 Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on less than 3% of parietale. Eastern Nearctic Region ..... 2
- 1' Epicranial suture subequal or longer than outer sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on 5% or more of parietale ..... 4
- 2 (1) Parietale mostly dark except behind eyes. Pointed microsculpture present near suture of mesonotum and metanotum ..... *E. lindrothi* new species p. 264
- 2' Parietale mostly pale except near suture of parietale and base of antennae. Pointed microsculpture absent from sutural portion of mesonotum and metanotum ..... 3
- 3 (2') Nasale with teeth. Pointed microsculpture present ventro-laterally on 3% of parietale. Darker pattern on dorsal surface of parietale extended along occipital suture. Pointed microsculpture present on entire surface of abdominal sternite 10 ..... *E. fuliginosus* Say p. 260
- 3' Nasale without teeth. Pointed microsculpture absent from ventro-lateral surface of parietale. Darker pattern on dorsal surface of parietale not extended to occipital suture. Pointed microsculpture absent from abdominal sternite 10 ..... *E. cicatricosus* LeConte p. 262
- 4 (1') Meshes of microsculpture absent from pronotum ..... 5
- 4' Meshes of microsculpture present on 5% or more of pronotum ..... 6
- 5 (4) Meshes of microsculpture of parietale restricted baso-laterally (5 to 10% of dorsal surface); pointed microsculpture of parietale restricted baso-laterally (5% of dorsal and ventral surface). Palearctic Region ..... *E. cupreus* Duftschmid p. 268



- 5' Meshes of microsculpture of parietale widespread baso-laterally (20% of dorsal surface); pointed microsculpture of parietale widespread baso-laterally (10% of dorsal surface and 2% of ventral surface). Nearctic Region ..... *E. clairvillei* Kirby p. 271
- 6 (4') Pointed microsculpture of parietale restricted baso-laterally (5% of dorsal surface and 3% of ventral surface). Seta AII-E of pronotum medium-sized. Pointed microsculpture of mesonotum and metanotum widespread near suture (20% of surface) restricted laterally (5% of surface), and absent from posterior band. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276
- 6' Pointed microsculpture of parietale widespread baso-laterally (50% of dorsal surface and 15% of ventral surface). Seta AII-E of pronotum large. Pointed microsculpture of mesonotum and metanotum restricted near suture (10% of surface) and widespread laterally (35% of surface), and present on posterior band (60% of surface). California and westernmost Nevada ..... *E. laevigatus* LeConte p. 280

## Second Instar Larvae

- 1 Dorsal surface of parietale mostly pale, dark only near frontale and base of antennae. Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture absent from dorso-lateral surface of parietale. Urogomphus with nine or more accessory setae. Eastern Nearctic Region ..... 2
- 1' Dorsal surface of parietale mostly dark, pale behind eyes and/or base. Epicranial suture subequal or longer than outer sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on parietale (15% or more of dorsal surface). Urogomphus with less than nine accessory setae ..... 4
- 2 (1) Microsculpture present over mesonotum and metanotum; pointed microsculpture well developed near suture ..... *E. lindrothi* new species p. 264
- 2' Microsculpture absent from mesonotum and metanotum, or if present, then pointed microsculpture absent near suture ..... 3
- 3 (2') Sclerites moderately setose: pronotal epipleuron with one or two accessory setae, urogomphus of tergum 9 with about 14 accessory setae (Fig. 98b). Meshes of microsculpture clearly outlined on nota, terga and urogomphi ..... *E. fuliginosus* Say p. 260
- 3' Sclerites densely setose: pronotal epipleuron with seven accessory setae, urogomphus of tergum 9 with about 25 accessory setae (Fig. 99a). Meshes of microsculpture absent from nota, very restricted on terga, and suggested on urogomphi ..... *E. cicatricosus* LeConte p. 262
- 4 (1') Pointed microsculpture present near suture of mesonotum (2% of surface) and of metanotum (10% of surface), on lateral portion of mesonotum and

	metanotum (15% of surface), and on anterior band of tergum 9 (10% of surface) .....	4
4'	Pointed microsculpture absent from sutural portion of mesonotum and metanotum, absent from or present on lateral portion of both nota (10% of surface), and absent from anterior band of tergum 9 .....	6
5 (4)	Pointed microsculpture of membrane on ventral surface of abdomen not extending to sternites 2 to 7. Meshes of microsculpture absent or indistinctly outlined on 50% of disc of pronotum. Palaearctic Region .....	
	..... <i>E. cupreus</i> Duftschmid p. 268	
5'	Pointed microsculpture of membrane on ventral surface of abdomen extending to sternites 2 to 7. Meshes of microsculpture clearly outlined on 10% of disc of pronotum. Nearctic Region .....	
	..... <i>E. clairvillei</i> Kirby p. 271	
6 (4')	Pointed microsculpture of parietale moderately widespread baso-laterally (15% of dorsal surface and 3% of ventral surface). Meshes of microsculpture moderately widespread on pronotum (30% of surface), and on mesonotum and metanotum (40% of surface). Pointed microsculpture absent from lateral portion of nota. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada .....	
	..... <i>E. olivaceus</i> LeConte p. 276	
6'	Pointed microsculpture of parietale widespread baso-laterally (30% of dorsal surface and 10% of ventral surface). Meshes of microsculpture widespread on pronotum (75% of surface) and on mesonotum and metanotum (90% of surface). Pointed microsculpture present from lateral portion of mesonotum and metanotum (10% of surface). California or westernmost Nevada .....	
	..... <i>E. laevigatus</i> LeConte p. 280	

**Third Instar Larvae**

1	Dorsal surface of parietale mostly pale, dark only near frontale and base of antennae. Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture absent from dorsal surface of parietale. Urogomphus with nine or more accessory setae. Eastern Nearctic Region .....	2
1'	Dorsal surface of parietale mostly dark, pale behind eyes and/or base. Epicranial suture subequal or longer than outer margin of antennomere 1. Pointed microsculpture moderately widespread on parietale (15% of dorsal surface). Urogomphus with less than nine accessory setae .....	4
2 (1)	Mesonotum and metanotum with pointed microsculpture near suture. Mesonotal and metanotal epipleuron with one to five accessory setae .....	
	..... <i>E. lindrothi</i> new species p. 264	
2'	Mesonotum and metanotum without pointed microsculpture near suture. Mesonotal and metanotal epipleuron without or with five to 15 accessory setae .....	3
3 (2')	Sclerites moderately setose: posterior band of mesonotum and metanotum without accessory setae, urogomphus with nine to 14 accessory setae (Fig. 98c). Meshes of microsculpture clearly outlined over most of nota and	

- terga ..... *E. fuliginosus* Say p. 260
- 3' Sclerites densely setose; posterior band of mesonotum and metanotum with five to 15 accessory setae laterally, urogomphus with about 30 accessory setae (Fig. 99b). Meshes of microsculpture absent from nota and very restricted on terga ..... *E. cicatricosus* Leconte p. 262
- 4 (1') Meshes of microsculpture absent from disc of pronotum. Pointed microsculpture present on lateral portion of mesonotum and metanotum (10% of surface), and on anterior band of tergum 9 (60% of band surface). Abdominal sternite 9 with about six accessory setae. Pointed microsculpture present on posterior band of terga 1 to 8 (5% or more of surface) ..... 5
- 4' Meshes of microsculpture present on pronotum (10% or more of surface). Pointed microsculpture absent from mesonotum, metanotum, and anterior band of tergum 9. Abdominal sternite 9 with two accessory setae. Pointed microsculpture absent from posterior band of terga 1 to 8. Nearctic Region ..... 6
- 5 (4) Pointed microsculpture absent from sutural area of mesonotum, present on metanotum (3% of surface). Palearctic Region ..... *E. cupreus* Duftschmid, p. 268
- 5' Pointed microsculpture near suture on 10% of disc of mesonotum and metanotum. Nearctic Region ..... *E. clairvillei* Kirby p. 271
- 6 (4') Meshes of microsculpture restricted: 10% of pronotum, and 40% of mesonotum and metanotum. Pointed microsculpture absent from anterior band of terga 1 to 8. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276
- 6' Meshes of microsculpture widespread: 75% of pronotum, and on 90 to 100% of mesonotum and metanotum. Pointed microsculpture present on 5% or more of anterior band of terga 1 to 8. California to westernmost Nevada ..... *E. laevigatus* LeConte p. 280

### THE ULIGINOSUS GROUP

#### Adults

*Diagnostic combination*.—Fringe of setae on posterior margin of pronotum terminated near middle of postero-lateral impression or nearer hind angle (Fig. 17a); lateral margin of pronotum wide, depressed in lateral view, pronotal epipleuron narrowest near middle (Fig. 17b); bead of lateral margin of pronotum 20 to 30 microns in width. Tibia of foreleg in males without projection at base of apical and posterior spur. Punctures of proepisternum 25 to 30 microns in diameter, and surrounding surface not impressed.

The five species of this group are restricted to the temperate and boreal areas of the Palearctic Region. Larvae of species of this group are not known.

*Elaphrus splendidus* Fischer von Waldheim

Fig. 41a-d

*Elaphrus splendidus* Fischer von Waldheim; 1828:267. Type area: Mongolia: type not seen. Motschulsky, 1846:71. Solsky, 1872:233. Marseul, 1880:29. 1882:4. Jacobson, 1906:267. Bänniger, 1919:147.

*Elaphrus splendidulus* Motschulsky, 1850b:LXVII. New Synonym.

**Adults**

**Diagnostic combination.**— Distinguished from adults of other species of group by brilliant green color on dorsal body surface, and by four rows of sharply outlined mirrors on the elytron.

**Description.**— Dorsal body surface (including pits) brilliant metallic green except for brilliant black mirrors; ventral surface dark metallic golden green; appendages black except femora with metallic green hue. Pronotum without small impressions antero-laterally. Elytral pits shallowly impressed, lateral ridges narrowly outlined or absent. Mirrors clearly outlined on intervals 3, 5, 7 and 9.

**Integument sculpture.** Punctures 30 to 40 microns in diameter on ventral body surface and on elytral intervals 4, 6 and 8, and 20 to 25 microns in diameter on pronotum and head. Distribution of punctures as in that of *E. uliginosus* but punctures denser on intervals 4, 6 and 8.

Microsculpture absent from or indistinctly outlined on intervals 4, 6 and 8, absent from or present in spots on pronotum.

**Male genitalia.** Apex of median lobe in dorsal view not twisted, thin-edged (30 microns in width) (Fig. 41a), in lateral view with apex slightly enlarged as in *E. uliginosus* but relatively wider (Fig. 41b).

**Measurements and proportions.**— Based on four specimens from Omsulcschan in northeastern Siberia. PL, 1.8-1.94-2.0 mm; 2.1-2.33-2.4 mm; EL, 4.6-4.98-5.1 mm; EW, 1.7-1.8-1.9 mm; HW, 2.0-2.11-2.2 mm; PL/PW 0.816-0.834-0.854; PL/EL, 0.385-0.389-0.398; PL/EW, 1.05-1.08-1.12; PL/HW, 0.867-0.920-1.0; PW/EL, 0.462-0.467-0.476; PW/EW, 1.28-1.29-1.32; PW/HW, 1.04-1.10-1.17; EL/EW, 2.71-2.77-2.82; EL/HW, 2.24-2.36-2.51; EW/HW, 0.807-0.852-0.890.

**Distribution.**— Kryzhanovskij (*in litt.*) reported adults of this species from Mongolia (Khentei Mts.) and Eastern Siberia to Kamchatka (from Irkutsk to Amur and Ussuri Rivers, Kamchatka, and Commander Is.).

**Taxonomic notes.**— Motschulsky's name was created by accidentally modifying Fischer's name and describing the species briefly. This made the name valid.

I have seen four specimens from Omsulcschan in northeastern Siberia, and dissected the only male.

**Geographical affinities.**— The range of this species overlaps with that of *E. sibiricus* and perhaps with that of *E. cupreus*.

*Elaphrus japonicus* Uéno

Fig. 42a-b

*Elaphrus cupreus* Habu; 1953:19 (*In*: Uéno, 1954) (*nec* Duftschmidt, 1812:194).

*Elaphrus sibiricus* Uéno; 1953:51 (*In*: Uéno, 1954) (*nec* Motschulsky, 1846:71).

*Elaphrus japonicus* Uéno, 1954:718. Type locality: Takinomata, Takedate, Aomori Prefecture, Japan; type not seen. Nakane, et. al., 1963:18. Ohkura, 1973:5.

**Adults**

**Diagnostic combination.**— Distinguished from adults of other species of group by scattered punctures on dorsal body surface (100 to 150 microns apart on intervals 4, 6 and 8), and by dark brown dorsal surface of body with copper reflections.

**Description.**— Dorsal body surface dark brown with copper luster except for purple pits; ventral body surface black with metallic golden hue; tibiae piceous and tarsomeres dark blue dorsally.

Impressions of pronotum numerous, as in *E. uliginosus*. Pits of elytra deeply impressed, lateral ridges wide and prominent. Elytral mirrors sharply outlined and slightly contrasted in intervals 3 and 5.

*Integument sculpture.* Punctures 20 to 25 microns in diameter on dorsal body surface, and 30 to 40 microns in diameter on ventral body surface. Punctures on dorsal body surface scattered: 100 to 150 microns apart on intervals 4, 6 and 8.

Microsculpture flat, over most of surface of body.

*Male genitalia.* Apex of median lobe in dorsal view (Fig. 42a) straight, thin-edged (30 microns in width), in lateral view with apex enlarged ventrally (Fig. 42b).

*Measurements and proportions.*— Based on two specimens from Aomori Pref., Japan. PL, 1.8-1.9 mm; PW, 2.1-2.3 mm; EL, 4.6-4.9 mm; EW, 1.7-1.8 mm; HW, 2.2-2.3 mm; PL/PW, 0.835-0.847; PL/EL, 0.388-0.391; PL/EW, 1.04-1.07; PL/HW, 0.828-0.835; PW/EL, 0.462-0.464; PW/EW, 1.25-1.27; PW/HW, 0.977-1.000; EL/EW, 2.68-2.75; EL/HW, 2.11-2.15; EW/HW, 0.770-0.802.

*Distribution.*— Adults are reported from Honshu Island, Japan and the Soviet far east (Kryzhanouskij, *in litt.*) from Middle Amur and Khabarousk to Vladivostok. I have seen specimens from Takedate-mura, Aomori Pref. (UASM, HGou).

*Taxonomic notes.*— I studied and dissected two males.

*Geographical affinities.*— The ranges of this species and *E. splendidus* probably overlap.

### *Elaphrus uliginosus* Fabricius

Figs. 17a-b, 43a-b, 119, 137

*Elaphrus uliginosus* Fabricius, 1792:178. Type locality: Germany; type not seen (see "Taxonomic notes"). Fabricius, 1801:245. Latreille, 1806:227. Gyllenhal, 1810:6. Dejean, 1826:269. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Küster, 1846:7. Letzner, 1849:50. Fairmaire and Laboulbène, 1854:6. Schaum, 1856:70. Stierlin, 1869:10. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Marseul, 1880:30. Sahlberg, 1880:10. Bedel, 1881:23. Fauvel, 1882:82. Marseul, 1882:4. Redtenbacher, 1874:6. Seidlitz, 1891:19. Ganglbauer, 1892:123. Semenov, 1895:312. Everts, 1898:49. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhn, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Obenberger, 1917:9. Porta, 1923:78. Louvet, 1925:17, 20. Portevin, 1929:41. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:218. Lindroth, 1974:33.

*Elaphrus riparius* Olivier, 1790:4. Rossi, 1790:193. Geoffroy, 1799: 156 (*ex parte*). Latreille, 1804:217. 1806:227. Gyllenhal, 1810:6. 1827:397. *nec* Linnaeus, 1758.

*Elaphrus latithorax* Schönherr, (*In*: Dejean, 1826). Dejean, 1826:270. Semenov, 1895:312. NOMEN NUDUM.

*Elaphrus impressifrons* Chaudoir, 1842:815. Type locality: Lac Ladoga, Baschkiria, USSR; type not seen. Motschulsky, 1850a:5. Marseul, 1882:4. Semenov, 1895:312. Jacobson, 1906:267.

*Elaphrus italicus* Dalla-Torre, 1877:23. Type locality: Italy; type not seen. Semenov, 1895:312. Jacobson, 1906:267.

*Elaphrus uliginosus* var. *italicus*; Schilsky, 1889:194.

*Elaphrus uliginosus purkynei* Obenberger, 1917:9. Type locality: Cepelare, Bulgaria; type not seen. Louvet, 1925:20.

*Elaphrus uliginosus laevisculptus* Bänninger, 1919:147. Type locality: Tien-shan; type not seen. Louvet, 1925:20.

*Elaphrus cupreus laevisculptus* Reitter (*In*: Bänninger, 1919). NOMEN NUDUM.

*Elaphrus bedeli* Méquignon, 1924:127. Type locality: Scalas, France; type not seen. Louvet, 1925:20. Jeannel, 1941:218.

*Elaphrus viridicupreus* Louvet, 1925:18. Type locality: Sedan, France; type not seen. Jeannel, 1941:218.

## Adults

*Diagnostic combination.*— Distinguished from adults of *E. pyrenoeus*, by dark green or copper dorsal surface of body, by sharply outlined meshes of microsculpture on intervals 4, 6 and 8. (Fig. 137) and by moderately impressed elytral pits (Fig. 119). Distinguished from remaining species of group by characters in key.

*Description.*— Dorsal body surface dark green or copper, rarely brilliant green, elytral pits purple; ventral body surface with dark metallic green or blue reflections; legs dark purple except for dark golden green femora.

Pronotum with postero-submedial impression in most specimens, and with two small impressions antero-lateral to main submedial impression. Elytral pits slightly impressed or not, lateral ridges clearly outlined except for specimens from western Himalaya. Mirrors sharply outlined and flat in interval 3, indistinctly outlined in intervals 7 and 9. Intervals 4, 6 and 8 in most specimens subcostate.

Table 3. Descriptive statistics for *E. uliginosus* based on 10 males and 10 females from central France and Switzerland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.4	2.08	0.185	0.054	5.8
PW	2.2–2.6	2.41	0.205	0.061	5.7
EL	4.7–5.5	5.10	0.381	0.114	5.0
EW	1.7–2.1	1.87	0.167	0.050	5.9
HW	2.2–2.6	2.33	0.164	0.049	4.7
B. Proportions					
PL/PW	0.816–0.888	0.864	0.030	0.009	2.3
PL/EL	0.381–0.427	0.409	0.019	0.006	3.2
PL/EW	1.050–1.170	1.110	0.056	0.017	3.4
PL/HW	0.833–0.938	0.894	0.040	0.012	2.9
PW/EL	0.446–0.500	0.474	0.019	0.006	2.7
PW/EW	1.240–1.350	1.290	0.057	0.017	3.0
PW/HW	0.989–1.090	1.030	0.049	0.015	3.2
EL/EW	2.570–2.830	2.720	0.105	0.031	2.6
EL/HW	2.100–2.310	2.190	0.086	0.026	2.6
EW/HW	0.750–0.856	0.804	0.039	0.012	3.3

*Integument sculpture.* Punctures 20 to 25 microns in diameter on head, on pronotum and on elytral intervals, and 30 to 40 microns in diameter on thoracic pleura and abdominal sterna. Punctures 30 to 40 microns apart on elytral intervals 4, 6 and 8, and on thoracic pleura; punctures of proepisternum 30 to 40 microns apart.

Microsculpture flat on dorsal surface except on mirrors, and convex in elytral pits and near postero-lateral angles of pronotum.

*Male genitalia.* Apex of median lobe in dorsal view twisted (Fig. 43a), thick-edged (65 microns), in lateral view with apex slightly enlarged (Fig. 43b).

*Measurements and proportions.*— Four samples studied, and data for two presented in tables 3 and 4.

*Variation.*— Specimens from central Europe, Ural Mountains in USSR and Tien-shan Mountains (USSR and China) do not differ significantly in means of measurements and proportions. However, specimens from Tien-shan Mountains seem smoother because the elytral pits are only slightly impressed, and because the lateral ridges of pits are indistinctly outlined. Thus, I assume there is gene flow or that gene flow was interrupted recently. However, the darker adults of the Italian sample differ significantly in the means of EL/HW and PW/HW and in their smaller size (EL, EW, PL and PW) from the above three samples. I feel that this mountain form is not connected by gene flow to the main French population, but my sample is too limited to confirm this. I have not seen specimens from the Balkan Mountains, but some of the character states in Obenberger's description (*in* Louvet, 1925) suggest that the Balkan specimens might represent a mountain race: pronotum and elytra more coarsely punctate; elytra shorter, elytral pits slightly impressed; dorsal body surface dark green or blue.

*Distribution.*— This Palearctic species ranges from the Atlantic Coast (Scandinavia to central France) across Russia, northern Italy (Apennine Mountains) Bulgaria (Balkan

Table 4. Descriptive statistics for *E. uliginosus* based on four males and seven females from central Italian Apennine Mountains.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.0	1.99	0.071	0.027	2.4
PW	2.1–2.4	2.27	0.135	0.054	4.0
EL	4.5–5.1	4.74	0.276	0.111	3.9
EW	1.7–1.8	1.76	0.092	0.037	3.5
HW	2.2–2.4	2.29	0.102	0.041	3.0
B. Proportions					
PL/PW	0.844–0.920	0.873	0.038	0.015	2.9
PL/EL	0.402–0.445	0.419	0.018	0.007	2.8
PL/EW	1.070–1.190	1.130	0.050	0.020	3.0
PL/HW	0.840–0.910	0.867	0.030	0.012	2.3
PW/EL	0.465–0.495	0.480	0.014	0.006	2.0
PW/EW	1.250–1.340	1.300	0.045	0.018	2.3
PW/HW	0.966–1.020	0.994	0.031	0.012	2.0
EL/EW	2.620–2.790	2.700	0.078	0.031	1.9
EL/HW	2.000–2.150	2.070	0.067	0.027	2.1
EW/HW	0.723–0.807	0.768	0.034	0.014	3.0

Mountains), southern Russia (Caucasus), east to Western Siberia (Yenisey River), and westernmost China (Tien-shan Mountains). The report of this species from the Amur River (Louvét, 1925) requires confirmation. Kryzhanouskij (*in litt.*) observed a similar distribution. I have seen specimens from: France, Italy, Switzerland, Austria, Germany, Denmark, Sweden, Poland, USSR as far east as the Tien-shan Mountains.

*Collecting notes.*— Adults occur on wet, sandy loam with abundant mosses (*Amblystegium*, *Paludela*, rarely *Sphagnum*); small bullrushes (Juncaceae), sedges (*Carex* spp.) and *Myrica gale* (Lindroth, 1945) are also generally present.

*Taxonomic notes.*— The type series was not available for study, but S.G. Larson determined two specimens as *E. cupreus* and one as *E. uliginosus* (Zimsen, E., 1964). Larson (Zimsen, 1964) did not designate a lectotype. Since I did not see the specimens, I prefer not to designate a lectotype. However, Fabricius (1792,1801) describes adults as greenish-bronze. Thus, Fabricius was not referring to *E. cupreus*, but to *E. uliginosus* as understood traditionally. Schonherr did not describe *E. latithorax*, but Dejean saw the labelled specimen and used the name. Specimens of *E. bedeli* and *E. viridicupreus* probably represent the copper and brilliant green forms of the typical *E. uliginosus* in France. I have seen specimens of *E. uliginosus* from the Ural region and I assume that *E. impressifrons* is the same species. *E. italicus* probably refers to the Italian Apennine form, *E. uliginosus purkynei* refers to the Balkan population, and *E. uliginosus laevisculptus* refers to the populations inhabiting the mountains of Tien-shan in the western Himalaya. Xamheu (1898. 1901) described larvae supposedly of this species. However, his larvae cannot be assigned to *Elaphrus* (occipital suture lacking and nasale bidentate); moreover, the habitat described (streams) is most unlikely for

Table 5. Descriptive statistics for *E. pyrenaesus* based on 10 males and 10 females from the French and Spanish Pyrenees.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.1	2.00	0.118	0.035	3.9
PW	2.1–2.4	2.27	0.150	0.045	4.4
EL	4.2–5.1	4.71	0.320	0.095	4.5
EW	1.5–1.9	1.73	0.171	0.051	6.6
HW	2.0–2.3	2.18	0.124	0.037	3.8
B. Proportions					
PL/PW	0.856–0.930	0.879	0.032	0.010	2.4
PL/EL	0.404–0.456	0.425	0.020	0.006	3.2
PL/EW	1.060–1.330	1.150	0.084	0.025	4.9
PL/HW	0.878–0.964	0.916	0.031	0.009	2.3
PW/EL	0.450–0.511	0.484	0.023	0.007	3.2
PW/EW	1.220–1.430	1.310	0.078	0.023	3.9
PW/HW	1.000–1.080	1.040	0.035	0.011	2.3
EL/EW	2.530–3.000	2.710	0.158	0.047	3.9
EL/HW	2.070–2.240	2.160	0.079	0.023	2.4
EW/HW	0.723–0.828	0.796	0.040	0.012	3.3

this species.

I have seen 110 specimens, and dissected seven males.

*Geographical affinities.*— The range of this species overlaps with that of *E. cupreus*, a member of the *cupreus* group.

### *Elaphrus pyrenaeus* Motschulsky

Figs. 44a-b, 120, 138

*Elaphrus pyrenaeus* Motschulsky, 1850b:LXVI. Type locality: Pyrénées; type not seen.

*Elaphrus uliginosus* var. *pyrenaeus*; Laboulbène, 1850:LXVII.

*Elaphrus splendidus*; Gaubil, 1849:14 (*nec* Fischer von Waldheim, 1828).

*Elaphrus uliginosus* var. *pyrenaeus*; Fairmaire and Laboulbène, 1854:7. Fauvel, 1882:82. Marseul, 1882:4. Seidlitz, 1891:19. Semenov, 1895:312. Jacobson, 1906:267. Obenberger, 1917:9. Bänninger, 1919:147. Louvet, 1925:20. Jeannel, 1941:218. Invalid emendation.

*Elaphrus pyrenaeus*; Jeanne, 1966:16.

*Elaphrus pyrenaeus nevadensis* Jeanne, 1966:18. Type locality: Puerto de la Ragua, Sierra Nevada, Granada, 1850 m.; type in Jeanne's collection, Bordeaux France; type seen by me. NEW SYNONYM.

### Adults

*Diagnostic combination.*— Distinguished from adults of *E. fuliginosus* by brilliant metallic green or brown copper dorsal body surface, by lack or presence of suggested meshes of microsculpture on intervals 4, 6 and 8, and by deeply impressed elytral pits (Fig. 120).

*Description.*— Upper body surface brilliant metallic green or in few specimens brilliant brown copper; ventral surface metallic golden green; most surfaces of legs and palpi dark blue.



Pronotum relatively long: means of PL/PW and PL/HW significantly higher than those of samples of *E. uliginosus*. Elytral pits deeply impressed (Fig. 120), lateral ridges narrowly outlined or absent, and intervals 4, 6 and 8 not costate.

*Integument sculpture.* Punctures similar in distribution to that of *E. uliginosus* but finer dorsally and denser ventrally (most adjacent punctures in contact on proepisternum).

Meshes of microsculpture restricted: present near elytral shoulder, otherwise absent from or indistinctly outlined on intervals 4, 6 and 8 (Fig. 138).

*Male genitalia.* Apex of median lobe similar to that of males of *E. uliginosus*, but in dorsal view apex more twisted (Fig. 44).

*Measurements and proportions.*— Two samples studied, and one presented in Table 5.

*Variation.*— I found little noteworthy variation between the samples from the Pyrénées and the Sierra Nevada, but the latter sample consisted of only two specimens. Thus, until further material is obtained, I prefer not to recognize *E. pyrenoeus nevadensis*.

*Distribution.*— I have seen specimens from the French and Spanish Pyrénées and also the type from the Sierra Nevada. Jeanne (1966) reported them from the following Spanish provinces: Lérida, Huesca, Bases Pyrénées, Navarra, Leon, Oviedo and Segovia. Louvet (1925) reported them from the Alps and Beaujolais Mountains, but I have not seen these specimens.

*Collecting notes.*— Found in subalpine and alpine mossy bogs (Jeanne, 1966).

*Taxonomic notes.*— I have seen 32 specimens and dissected three males.

*Geographic affinities.*— This species is allopatric in relation to all other known member of *Neoelaphrus*.

### *Elaphrus potanini* Semenov

*Elaphrus potanini* Semenov, 1889:352. Type locality: China, Gan-ssu (Kansu in current spelling) at Amdo; type not seen. Jacobson, 1906:267.

### Adults

*Diagnostic combination.*— Distinguished from adults of other species of subgenus by brilliant brown color of dorsal body surface, and by metallic green elytral pits.

*Description.*— Dorsal body surface brown with copper luster; elytral pits, postero-lateral angles of pronotum, and anterior portion of head metallic green; antennomeres 1 to 3, femur (except base), base of tibia, and dorsal surface of tarsomeres metallic golden-green; base of femur and middle of tibia dark reddish brown; palpi brown.

Pronotum transverse and wider than head; lateral margin deeply sinuate; postero-lateral angles rather prominent and acute; anterior transverse stria deeply impressed near middle; main discal impression slightly impressed; medial stria deep and short. Elytra elongate, pits well impressed, lateral ridges obsolete; mirrors not sharply outlined in intervals 3 and 5.

*Integument sculpture.* Punctures fine and dense over most of dorsal body surface. Microsculpture undescribed.

*Male genitalia.* Undescribed.

*Distribution.*— The type specimen is from the Chinese province fo Kansu at Amdo, collected on May 22, 1885.

*Taxonomic notes.*— This species is known to me only through Semenov's description. I included it in this group because of the deeply impressed anterior transverse stria of the pronotum, and also the transverse pronotum that is wider than the head. I believe that it represents a distinct species because of its unusual coloration, and its short and transverse pronotum. Based on previous experience with Semenov's species, I trust his judgement.

Besides the type, Kryzhanoskij (*in litt.*) reported three additional specimens.

*Geographical affinities.*— Probably allopatric in relation to all other known members of *Neoelaphrus*.

THE *FULIGINOSUS* GROUP

## Adults

*Diagnostic combination*.— Fringe of setae on posterior margin of pronotum ending 150 to 200 microns from postero-lateral angles (Fig. 18a); lateral margin of pronotum, in lateral view, not depressed near middle, pronotal epipleuron not narrowest at middle (shaped as in Fig. 18b); bead of lateral margin of pronotum 20 to 30 microns in width, or lacking. Tibia of foreleg of male with one small projection at base of apical spur and one large projection at base of posterior spur--best seen in posterior view (Fig. 149). Punctures of proepisternum 30 to 45 microns in diameter, area near punctures widely depressed (diameter of depression about 80 microns)--best seen on proepisternum (Fig. 107).

## All Instar Larvae

*Diagnostic combination*.— All instars: epicranial suture subequal to inner edge of antennomere 1; pointed microsculpture lacking or slightly developed baso-laterally.

Second and third instar larvae: parietale mostly pale except near frontale suture, and without pointed microsculpture dorso-laterally; urogomphus with nine or more accessory setae.

The three species of this group are restricted to the temperate Nearctic region.

*Elaphrus fuliginosus* Say

Figs. 18a-b, 45a-b, 158

*Elaphrus fuliginosus* Say, 1834:417. Type locality: originally Pennsylvania, but Lindroth and Freitag (1969) designated a male neotype from Rumney, New Hampshire; neotype in Museum of Comparative Zoology, Massachusetts; neotype seen by me. Crotch, 1873:4. 1876:246; Schaupp, 1878:6. Blatchley 1910:48. Lindroth, 1961:114.

*Elaphrus clairvillei*; LeConte, 1848:448 (*nec* Kirby, 1837). Crotch, 1873:4. 1876:246. Schaupp, 1878:6.

## Adults

*Diagnostic combination*.— Distinguished from adults of *E. cicatricosus* and *E. lindrothi* by well developed and wide (20 to 30 microns) bead on lateral margin of pronotum, and by dark metallic green color of dorsal surface. Specimens of *E. fuliginosus* are likely to be confused with some members of the *uliginosus* group (especially with specimens of *E. uliginosus*). Distinguished from *E. uliginosus*, by green tibiae and tarsomeres.

*Description*.— Dorsal body surface dark green except for purple pits; ventral body surface dark golden-green, but abdomen piceous; legs and palpi brown or reddish-brown with a metallic green hue.

Lateral margin of pronotum completely beaded; pronotum with sharply impressed median longitudinal and anterior transverse striae; disc with two pairs of weakly suggested impressions antero-laterally. Mirrors of elytral intervals 3 and 5 sharply outlined, and markedly contrasted against microsculptured, green, and densely punctate intervals 4 and 6. Elytral pits moderately impressed, with narrow lateral ridges and with 20 to 25 punctures. Abdominal sternum 7 of males with numerous accessory setae, and of females with fewer than four.

Trochanter of foreleg with two setae. Femur of foreleg, midleg and hindleg with about 60, 60, and 10 setae respectively. Tibia of foreleg, midleg and hindleg with about 25, 80, and 80 setae respectively.

*Integument sculpture*. Punctures 20 to 30 microns in diameter on coxae and scutellum, 30 to 40 microns in diameter on clypeus, on head, on pronotum and elytral intervals, and 40 to 45 microns in diameter on pleura and sterna. Punctures 20 to 80 microns apart on dorsal body surface, and on average 40 microns apart on thoracic sterna and pleura, 40 to 120 microns apart laterally on abdominal sterna.

Microsculpture flat on dorsal surface except on mirrors, and convex in elytral pits and near postero-lateral angles of pronotum.

*Male genitalia*. Apex of median lobe in dorsal view thin-edged (Fig. 45a), and in lateral view with angular projection ventrally (Fig. 45b).

*Measurements and proportions*.— Two samples studied, and data for one presented in Table 6.

Table 6. Descriptive statistics for *E. fuliginosus* based on 10 males and 10 females from Brooklyn, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	2.0–2.4	2.23	0.188	0.097	4.7
PW	2.2–2.6	2.45	0.143	0.043	3.9
EL	4.5–5.4	5.00	0.349	0.104	4.6
EW	1.5–2.0	1.84	0.139	0.041	5.0
HW	2.3–2.7	2.51	0.156	0.047	4.1
<b>B. Proportions</b>					
PL/PW	0.875–0.942	0.915	0.023	0.007	1.6
PL/EL	0.426–0.458	0.442	0.014	0.004	2.1
PL/EW	1.170–1.260	1.210	0.039	0.012	2.1
PL/HW	0.840–0.916	0.891	0.031	0.009	2.3
PW/EL	0.462–0.495	0.483	0.014	0.004	1.9
PW/EW	1.280–1.390	1.320	0.040	0.012	2.0
PW/HW	0.941–1.000	0.974	0.026	0.008	1.8
EL/EW	2.670–2.810	2.740	0.061	0.018	1.5
EL/HW	1.960–2.080	2.020	0.051	0.015	1.7
EW/HW	0.713–0.772	0.735	0.024	0.007	2.2

*Variation.*— I found no significant differences between two distant samples: one from Manitoba and Minnesota, and one from Brooklyn, New York. Specimens of the western sample were slightly larger on average.

#### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species of the group as follows: nasale toothed; pointed sculpture present near suture of mesonotum and metanotum.

#### First Instar Larvae

*Description.*— Dorsal surface of parietale pale except anteriorly near antennae, along frontale and occipital sutures. Nasale toothed. Pointed sculpture of parietale restricted baso-laterally (5% of dorsal surface). Meshes of microsculpture present on 15% of each sclerite of mesonotum and metanotum; pointed sculpture present near suture of both nota.

#### Second Instar Larvae

*Description.*— Pronotal epipleuron with one or two accessory setae; pronotum with meshed microsculpture on 10% of surface. Mesonotal epipleuron with one accessory seta; meshed microsculpture present on 40% of mesonotum, pointed microsculpture restricted to lateral portion (10% of surface). Metathorax as mesothorax. Each sclerite of terga 1 to 8 with about 25 accessory setae, and urogomphus with nine (Fig. 98b). Pointed microsculpture restricted on tergum 1, widespread on terga 2 to 8, clearly outlined and shaped as small scales on urogomphus, and multipointed on tergum 10. Pointed microsculpture restricted to lateral portion of posterior bank of terga 1 to 8 (5% of surface), and of anterior band of tergum 9 (10% of surface). Epipleuron and hypopleuron of terga 2 to 8 each with about eight accessory setae. Sternite of abdominal segment 8 with about 15 accessory setae.

### Third Instar Larvae

*Description.*— Each sclerite of pronotum with about 20 accessory setae; meshes of microsculpture absent from disc. Each sclerite of mesonotum with about 85 accessory setae. Mesosternite without accessory setae. Largest projection of urogomphus in lateral view large (Fig. 98c); each sclerite of terga 1 to 8 with about 70 accessory setae, and urogomphus with nine; pointed microsculpture on 5% of anterior band of terga 1 to 8, and on 20% of anterior band of tergum 9; microsculpture barely suggested on urogomphus. Epipleuron of segments 2 to 8 with about 30 accessory setae. Hypopleuron of segments 1 to 8 with about 25 accessory setae. Outer poststernite of segment 1 with about eight accessory setae, and of segments 2 to 7 with about 14. Inner poststernite of segment 1 with two accessory setae, and of segments 2 to 7 each with four.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— From the Atlantic coast of Maine to Maryland, west to Manitoba and Nebraska (Fig. 158).

*Collecting notes.*— According to Larochelle (1975) adults are found in open places with sparse vegetation on wet sandy soil. I found two specimens in a similar habitat.

*Taxonomic notes.*— I examined 275 adults, and dissected five males. I studied three first instar, one second instar, and one third instar larvae from Vermont.

*Geographical affinities.*— The range of this species overlaps with that of all species of the *uliginosus* group at least in Maryland, and with those of *E. clairvillei* and *E. olivaceus* in the northern half of its range.

### *Elaphrus cicatricosus* LeConte

Figs. 47a-b, 99a-b, 107, 139, 145, 146, 147, 148, 149, 150, 159

*Elaphrus cicatricosus* LeConte 1848:448. Type locality: Central New York State; type in Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts; type seen by me. LeConte 1853:402. Crotch, 1873:4. 1876:246. Schaupp: 1878:6. Lindroth, 1961:114.

*Elaphrus rhodeanus* Casey, 1924:17. Type locality: Boston Neck, Rhode Island; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington D.C. Lindroth, 1961:114.

### Adults

*Diagnostic combination.*— Distinguished from adults of other species of the group by unbeaded lateral margin of pronotum and by large lateral ridges in pits of elytra.

*Description.*— Dorsal body surface dark brown with copper luster except for purple pits; ventral surface black but abdominal sterna dark piceous; legs brown with green metallic hue on femur and blue metallic hue on tibia and tarsomeres. Lateral margin of pronotum unbeaded; pronotum with sharply impressed medial stria and indistinctly outlined anterior transverse stria; disc without antero-lateral impression. Mirrors of elytral intervals 3 and 5 sharply outlined, but little contrasted against dark and sparsely punctate intervals 4 and 6. Elytral pits deeply impressed, with large and convex lateral ridges, and with four to eight punctures. Abdominal sternum 7 of males and females without or with one or two accessory setae.

Trochanter of foreleg with one seta. Femur of foreleg, midleg and hindleg with about 30, 30 and six setae respectively. Tibia of foreleg, midleg and hindleg with about 20, 55 and 55 setae respectively.

*Integument sculpture.* Punctures 20 to 30 microns in diameter on coxae, 30 to 40 microns in diameter on dorsal body surface, and 40 to 45 microns in diameter on ventral body surface. Punctures 10 to 200 microns apart on dorsal body surface, 10 to 90 microns apart on pleura, and 70 to 150 microns apart on sterna.

Microsculpture subconvex on dorsal body surface, convex in elytral pits, and near postero-lateral impression of pronotum, and flat on ventral body surface.

*Male genitalia.* Apex of median lobe in dorsal view thick-edged (Fig. 47a), and in lateral view with round and weak ventral projection (Fig. 47b).

*Measurements and proportions.*— Two samples studied, and data for one presented in Table 7.

Table 7. Descriptive statistics for *E. cicatricosus* based on 10 males and 10 females from Maclean Bog, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	2.0–2.3	2.11	0.116	0.035	3.7
PW	2.2–2.5	2.32	0.135	0.040	3.9
EL	4.5–5.2	4.86	0.270	0.080	3.7
EW	1.6–1.9	1.79	0.129	0.038	4.8
HW	2.3–2.6	2.44	0.106	0.032	2.9
<b>B. Proportions</b>					
PL/PW	0.872–0.966	0.909	0.033	0.010	2.4
PL/EL	0.422–0.454	0.435	0.019	0.005	2.4
PL/EW	1.130–1.240	1.190	0.050	0.015	2.8
PL/HW	0.828–0.911	0.865	0.026	0.008	2.0
PW/EL	0.454–0.510	0.479	0.020	0.006	2.7
PW/EW	1.250–1.370	1.310	0.061	0.018	3.1
PW/HW	0.907–0.990	0.952	0.030	0.009	2.1
EL/EW	2.620–2.840	2.740	0.099	0.029	2.4
EL/HW	1.900–2.060	1.990	0.065	0.019	2.2
EW/HW	0.697–0.767	0.726	0.032	0.009	2.9

*Variation.*— I found no significant differences between means of samples from northern New York and New Jersey.

### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species of the group by lack of teeth on nasale, and of microsculpture near suture of mesonotum and metanotum.

### First Instar Larvae

*Description.*— Dorsal surface of parietale pale except anteriorly near antennae and along suture of frontale. Nasale not toothed. Pointed microsculpture absent from parietale. Meshes of microsculpture present on 10 to 12% of each sclerite of mesonotum and metanotum; pointed microsculpture lacking on both nota.

### Second Instar Larvae

*Description.*— Pronotal epipleuron with seven accessory setae; pronotum without microsculpture. Mesonotal epipleuron with five accessory setae; mesonotum without microsculpture. Metathorax as mesothorax. Each sclerite of terga 1 to 8 with 36 accessory setae, and urogomphus with 25 (Fig. 99a). Pointed microsculpture of terga 1 to 8 restricted (5% of surface), indistinct on urogomphus, and single-pointed on tergum 10. Pointed microsculpture absent from posterior band of terga 1 to 8, and from anterior band of tergum 9. Epipleuron and hypopleuron of segments 1 to 8 each with about 25 accessory setae. Sternite of abdominal segment 8 with about 22 accessory setae.

### Third Instar Larvae

*Description.*— Each sclerite of pronotum with about 40 accessory setae; meshes of microsculpture absent from disc. Each sclerite of mesonotum with more than 100 accessory setae. Mesosternite with three accessory setae. Largest projection of urogomphus medium-sized in lateral view. (Fig. 99b); terga 1 to 8 each with about 140 accessory setae, and

urogomphus with about 30; pointed microsculpture absent from anterior band of terga 1 to 9; microsculpture absent from urogomphus. Epipleuron of segments 2 to 8 with 40 to 60 accessory setae. Hypopleuron of segments 1 to 8 with 25 to 50 accessory setae. Outer poststernite of segment 1 with about 15 accessory setae, and of segments 2 to 7 with about 18. Inner poststernite of segment 1 with five accessory setae, and of segments 2 to 7 each with seven.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— The range of this species extends in the north from Michigan, southern Quebec and Maine, south to Tennessee and Maryland (Fig. 159).

*Collecting notes.*— I found these beetles in various localities on wet, relatively firm organic mud near slow-flowing brooks where alders grew commonly, usually in the shade of larger trees. These observations match well with those of Lindroth, Darlington (Lindroth, 1961:114), Frost (1910) and Masner (pers. comm.).

*Taxonomic notes.*— The type of *E. rhodeanus* matches typical specimens of *E. cicatricosus*.

I examined 250 adults and dissected four males. I studied three first instar, three second instar, and three third instar larvae from Maclean Bog, New York.

*Geographical affinities.*— The ranges of *E. fuliginosus* and this species nearly completely overlap. At the southeastern end of its range, this species is sympatric with *E. lindrothi*. In the northern half of its range, *E. cicatricosus* overlaps with those of *E. clairvillei* and *E. olivaceus*.

### *Elaphrus lindrothi* new species

Figs. 46a-b, 104, 121, 159

*Elaphrus lindrothi* new species. Type material: holotype male and allotype female labelled "Ill., Jackson Co., 3 mi. n. Pomona -- 37° 41' N 87° 20' W, 1, V, 79, H. Goulet"; type (No. 18010) in Canadian National Collection, Ottawa. Additional paratypes deposited in collections of CNCI, MCZC, USNM, UASM and CASC.

*Elaphrus cicatricosus*; Blatchley, 1910:49 (nec LeConte, 1848).

### Adults

*Diagnostic combination.*— Distinguished from adults of other species of group by unbeaded lateral margin of pronotum, and by barely suggested lateral ridges of the elytral pits.

*Description.*— Dorsal body surface dark silver; ventral body surface black or dark brown, but abdominal sterna brown; legs, palpi and antennomeres 1 to 3 reddish brown; femora, tibiae and tarsomeres with metallic purple hue.

Lateral margin of pronotum unbeaded; pronotum with weakly impressed medial longitudinal stria, and with sharply impressed anterior transverse stria; disc without antero-lateral impression. Mirrors of interval 3 weakly outlined, and contrasted against silver, and densely punctate intervals 2 and 4. Pits of elytra impressed, without or with barely suggested lateral ridges (Fig. 104), and with about 10 to 15 punctures. Abdominal sternum 7 of males and females without accessory setae.

Trochanter of foreleg with two setae. Femur of foreleg, midleg and hind leg with about 30, 30 and five setae respectively. Tibia of foreleg, midleg and hindleg with about 20, 55 and 55 setae respectively.

*Integument sculpture.* Punctures 20 to 25 microns in diameter on coxae, clypeus, head, pronotum and on elytral intervals, and 30 to 35 microns in diameter on pleura and sterna. Punctures 10 to 30 microns apart on head and on elytral intervals 4, 6 and 8 (Fig. 121), 20 to 40 microns apart on pronotum (Fig. 104), and 20 to 90 microns apart on ventral body surface.

Microsculpture subconvex on dorsal body surface, on pleura of prothorax and mesothorax, and flat on remaining ventral body surface.

*Male genitalia.* Apex of median lobe in dorsal view thin-edged (Fig. 46a), and in lateral view with angular ventral projection (Fig. 46b).

*Measurements and proportions.*— One sample studied. See Table 8.

*Variation.*— Except for those from Illinois, samples were too small for analysis. Samples on eastern and western extremes of the geographical range appear similar.

Table 8. Descriptive statistics for *E. lindrothi* new species based on three males and five females from southern Indiana and Maryland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.83	0.132	0.062	4.8
PW	1.7–2.1	1.87	0.195	0.092	6.6
EL	3.8–4.4	4.15	0.346	0.163	5.6
EW	1.5–1.7	1.61	0.148	0.070	6.1
HW	2.0–2.3	2.18	0.136	0.064	4.2
B. Proportions					
PL/PW	0.878–0.973	0.929	0.052	0.025	3.7
PL/EL	0.415–0.477	0.440	0.029	0.014	4.4
PL/EW	1.060–1.220	1.130	0.079	0.037	4.7
PL/HW	0.820–0.851	0.839	0.016	0.008	1.3
PW/EL	0.441–0.503	0.475	0.030	0.014	4.2
PW/EW	1.170–1.290	1.220	0.072	0.034	3.9
PW/HW	0.852–0.953	0.905	0.051	0.024	3.8
EL/EW	2.490–2.680	2.570	0.093	0.044	2.4
EL/HW	1.780–1.980	1.910	0.100	0.047	3.5
EW/HW	0.698–0.779	0.742	0.042	0.020	3.8

All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species of the group by lack of teeth on nasale, and by presence of pointed microsculpture near suture of mesonotum and metanotum.

First Instar Larvae

*Description.*— Parietale mostly dark except behind eyes. Nasale without teeth. Pointed microsculpture of parietale restricted baso-laterally (5 to 10% of dorsal surface). Meshes of microsculpture present over 50% of surface of mesonotum and metanotum; pointed microsculpture present along suture of both nota as wide bands (25% of surface).

Second Instar Larvae

*Description.*— Parietale dark near frontale and epicranial suture only. Pronotal epipleuron with two or three accessory setae; pronotum with meshes of microsculpture over surface. Mesonotal epipleuron with one or two accessory setae; meshed microsculpture present over most of mesonotum, and pointed microsculpture present laterally (10% of disc surface) and near suture (10% to 20% of disc surface). Each sclerite of terga 1 to 8 with about 25 accessory setae, and urogomphus with nine to 14. Pointed microsculpture developed on all of terga 1 to 8 and urogomphus, and single-pointed on tergum 10. Pointed microsculpture absent from posterior bands of terga 1 to 8, and present on anterior band of tergum 9 (5% of surface). Epipleuron and hypopleuron of segments 2 to 8 each with about 15 accessory setae. Sternite of segment 8 with 12 to 15 accessory setae.

Third Instar Larvae

*Description.*— Each sclerite of pronotum with about 40 accessory setae; meshes of microsculpture widespread but weakly outlined. Each sclerite of mesonotum and metanotum with more than 100 accessory setae. Mesosternite with two to three accessory setae. Largest projection of urogomphus in lateral view large (Fig. 98c); each sclerite of terga 1 to 8 with about 110 accessory setae, and urogomphus with nine to 14; pointed microsculpture absent from anterior band of terga 1 to

8, and present on anterior band of tergum 9 (5% of surface); microsculpture absent from urogomphus. Epipleuron of segments 2 to 8 with 40 to 60 accessory setae. Hypopleuron of segments 1 to 8 with 25 to 50 accessory setae. Outer poststernite of segment 1 with eight to 13 accessory setae, and of segments 2 to 7 with 18 to 20. Inner poststernite of segments 2 to 7 with three to six accessory setae.

### Geographical Distribution and Affinities, and Notes

*Derivation of specific epithet.*— I name this species in honor of the late Prof. C.H. Lindroth, who contributed immensely to a better understanding of North American carabids, and provided a solid base for further study of the Elaphrini.

*Distribution.*— Known from eastern United States (Fig. 159). Localities are listed below.

*United States.* MARYLAND: Priest Bridge (1:USNM), Bowie (2:USNM). INDIANA: Knox County (4:PURC), Hovey Lake (1:PURC). ILLINOIS: Union County (3:CNCI), Jackson County, 3 mi. n. Pomona (70: CASC, CNCI, MCZC, USNM, UASM).

*Collection notes.*— In Illinois, many adults were found in the shade of bald cypresses on clay flats, covered partly with rotted leaves. In springtime, before the cypresses are fully leafed, numerous *E. ruscarius* were found also in this habitat. This habitat is similar to those observed by Blatchley (1910) in southern Indiana for his "*E. cicatricosus*".

*Taxonomic notes.*— I examined 81 adults, and dissected four males. I studied seven first instar, three second instar, and three third instar larvae from Pomona, Illinois.

*Geographical affinities.*— The range of this species overlaps with those of *E. fuliginosus* and *E. cicatricosus*.

### THE CUPREUS GROUP

#### Adults

*Diagnostic combination.*— Fringe of setae on posterior margin of pronotum ending near postero-lateral impressions (200 microns or more from postero-lateral angles) (Fig. 19); lateral margin of pronotum, in lateral view, not depressed near middle, pronotal epipleuron not narrowest at middle (shaped as in Fig. 18b); bead of lateral margin of pronotum 10 to 15 microns in width. Tibia of foreleg of males without projection at base of apical and posterior spur. Punctures of proepisternum 25 to 30 microns in diameter, and surrounding surface narrowly impressed or not.

#### Larvae

*Diagnostic combination.*— All instars: epicranial suture subequal or longer than outer edge of antennomere 1; pointed microsculpture present baso-laterally on 5% or more of parietale dorsal surface.

Second and third instar larvae: parietale mostly dark except behind eye and/or base, and with pointed microsculpture dorso-laterally (15% or more of surface); urogomphus with seven accessory setae.

The five species of this group occur in temperate and boreal regions of the northern hemisphere.

#### *Elaphrus sibiricus* Motschulsky

Fig. 48a-b

*Elaphrus sibiricus* Motschulsky, 1846:71. Type locality: probably Irtysh River, USSR, type not seen. Solsky 1872:232, 233. Marseul, 1880:66. Bates, 1883:205, 217. Jacobson, 1906:267. Nakane, 1955:22. 1963:18.

*Elaphrus dauricus* Morawitz, 1863:191. Type locality: probably Dauria (region s.e. of Lake Baikal), USSR; type not seen. Solsky, 1872: 232, 233. Marseul, 1880:29. Jacobson, 1906:267.



Table 9. Descriptive statistics for *E. sibiricus* based on nine males and five females from eastern Siberia, northeastern China and northern Japan.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.1	1.98	0.150	0.053	5.0
PW	2.1–2.4	2.28	0.157	0.055	4.6
EL	4.5–5.2	4.89	0.256	0.091	3.5
EW	1.6–1.8	1.74	0.105	0.035	4.0
HW	2.1–2.4	2.27	0.120	0.043	3.5
B. Proportions					
PL/PW	0.805–0.910	0.869	0.045	0.016	3.5
PL/EL	0.385–0.421	0.404	0.015	0.005	2.5
PL/EW	1.060–1.180	1.130	0.054	0.019	3.2
PL/HW	0.841–0.899	0.871	0.029	0.010	2.2
PW/EL	0.437–0.480	0.466	0.017	0.006	2.5
PW/EW	1.260–1.330	1.300	0.034	0.012	1.7
PW/HW	0.943–1.050	1.000	0.047	0.017	3.1
EL/EW	2.740–2.880	2.800	0.072	0.028	1.7
EL/HW	2.090–2.220	2.150	0.056	0.020	1.7
EW/HW	0.742–0.811	0.769	0.031	0.011	2.7

*Elaphrus cupreus*; Solsky, 1872:233 (*nec* Duftschmid, 1812).

## Adults

**Diagnostic combination.**— Distinguished from adults of other species of the group by green tarsomeres; and by well developed meshes of microsculpture on elytral intervals 4, 6 and 8.

**Description.**— Upper body surface brilliant green in impressions, dark green or bronze-green elsewhere except for purple pits; ventral body surface dark golden-green to nearly black medially; legs and palpi piceous except for metallic green reflection on femora, apex of tibiae, and tarsomeres.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with two pairs of submedial impressions. Prosternal process with one to six accessory setae. Metasternum with few punctures medially; all punctures setose. Abdominal sterna 5 and 6 each with five to 10 accessory setae, sternum 7 in males with 10 to 20, and in females with 10 or less. Setigerous punctures of elytron distinctly outlined. Elytral pits well impressed, and with 10 to 15 punctures; lateral ridges of pits wide, and not fused anteriorly and posteriorly (Fig. 132). Mirrors sharply outlined and contrasted on intervals 3, or 3 and 5. Number of setae on legs not studied in detail, but similar to those of adults of *E. clairvillei*. Tibia of midleg of males with sharp apical projection at base of inner spur (Fig. 150). Hind coxa with punctures on outer half, and with eight to 15 accessory setae on inner half.

**Integument sculpture.** Punctures 25 to 35 microns in diameter on clypeus, head, pronotum and on elytral intervals 4, 6 and 8, 30 to 35 microns in diameter on pleura and laterally on thoracic and abdominal sterna. Punctures 30 to 50 microns apart on clypeus, head, lateral portions of pronotum, elytral intervals 4, 6 and 8, on pleura, and on lateral portions of thoracic and abdominal sterna.

Microsculpture on head, pronotum, elytral intervals 4, 6 and 8, pleura, and thoracic and abdominal sterna subconvex or convex.

**Male genitalia.** Apex of median lobe in lateral view wide and angular ventro-apically (Fig. 48b); in dorsal view, apex straight, thick-edged (40 microns), and extended far posteriorly from apex of internal sac (Fig. 48a).

**Measurements and proportions.**— One sample studied. See Table 9.

*Variation.*— I could not study this aspect as I had too few specimens.

*Distribution.*— The range of this species extends from central eastern Siberia and Mongolia, to northeastern China, northern Japan and Kamchatka. I have seen specimens from the following localities: USSR: Lake Baikal (BMNH, MCZ, UASM), Tschita (MCZ), Amur River (BMNH), and Ussuri River (MCZ); CHINA: Hailar (MCZ); JAPAN: Rebun Island. Kryzhanovskij (*in litt.*) reported adults from as far west as Krasnoyarsk and Yakutsk region (Jakutia) and from Kamchatka in the northeast.

*Collecting notes.*— One specimen was found on a stream bank (Ball pers. comm.). I have seen a slightly tanned male collected in mid-August. Thus adults probably overwinter.

*Taxonomic notes.*— According to the descriptions, adults of *E. dauricus* match those of *E. sibiricus*.

I studied nine males and five females, and dissected three males.

*Geographical affinities.*— Found sympatrically with *E. cupreus*, a member of the *cupreus* group, and with *E. splendidus* and *E. japonicus*, both members of the *uliginosus* group.

### *Elaphrus cupreus* Duftschmid

Figs. 19, 49a-b, 108, 132

*Elaphrus cupreus* Duftschmid, 1812:194. Type locality: probably Germany; type not seen. Dejean, 1826:271. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Schiøtte, 1841:356. Chaudoir, 1842:815. Küster, 1846:7. Letzner, 1849:50. Fairmaire and Laboulbène, 1845:6. Schaum, 1860:68. Stierlin, 1869:11. Redtenbacher, 1874:6. Seidlitz, 1875:2. Sahlberg, 1880:10. Bedel, 1881:23. Fauvel, 1882:81, 83. Marseul, 1882:4. Redtenbacher, 1874:6. Seidlitz, 1891:19. Ganglbauer, 1892:123. Everts, 1898:49. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhnt, 1912:50. Fairmaire, 1913:31. Schauffuss, 1916:29. Bänninger, 1919:148. Porta, 1923:78. Portevin, 1929:41. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:218. Lindroth, 1974:33.

*Elaphrus riparius*; Olivier, 1790:4 (*nec* Linnaeus, 1758). Dejean, 1826:271. Schaum, 1856:68. Marseul, 1882:4. Ganglbauer, 1892:123. Semenov, 1895:313. Jacobson, 1906:267. Jeannel, 1941:218.

*Elaphrus uliginosus*; Illiger 1798:225 (*nec* Fabricius, 1792). Dejean, 1826:271. Schaum, 1856:68. Ganglbauer, 1892:123. Semenov, 1895:313. Jacobson, 1906:267. Jeannel, 1941:218.

*Elaphrus arcticus*; Dejean, 1826:272. Type locality: Lapland; type not seen. Fauvel, 1882:83. Semenov, 1895:313. Bänninger, 1919:148.

*Elaphrus borealis* Andersch (NOMEN NUDUM). Gaubil, 1849:14. Motschulsky, 1850a:5. Semenov, 1895:313.

*Elaphrus cupreus* var. *arcticus*; Marseul, 1882:4. Jacobson, 1906:267.

*Elaphrus cupreus* var. *dauricus*; Marseul, 1882:4 (*nec* Morawitz, 1863).

## Adults

*Diagnostic combination.*— Distinguished from adults of other species of this group by dark brown copper color of the dorsal surface of body, by purple tibiae and tarsomeres and by well outlined meshes of microsculpture on head, pronotum and intervals 4, 6 and 8 (Fig. 132).

*Description.*— Upper body surface dark brown with copper luster except for purple pits; ventral body surface dark golden green; legs and palpi piceus except for dark green hue on femora, and purple on apex of tibiae and tarsomeres.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with two pairs of submedial impressions. Prosternal process with one to four accessory setae. Metasternum with few punctures antero-medially; most punctures setose. Abdominal sterna 5 and 6 each with five to 15 accessory setae, sternum 7 in males with about 20 and in females with five to 10. Setigerous punctures of elytron distinctly outlined. Pits of elytron deeply impressed, and with 10 to 25 punctures; lateral ridges wide and not fused anteriorly and posteriorly (Fig. 132). Mirrors sharply outlined and contrasted on intervals 3, or 3 and 5. Number of setae on legs not studied in detail, but similar to those of adults of *E. clairvillei*. Tibia of midleg of males with sharp apical projection at base of inner spur (Fig. 150). Hind coxae with few punctures on outer 0.5, and with three to five accessory setae near inner margin.

*Integument sculpture.* Punctures 15 to 25 microns in diameter on clypeus, head, pronotum and on elytral intervals 4, 6 and 8, 30 microns in diameter on pleura and lateral portions of thoracic and abdominal sterna. Punctures 50 to 150 microns apart on head, on lateral portion of pronotum, and on elytral intervals 4, 6 and 8, 30 to 50 microns apart on pleura, and lateral portion of thoracic and abdominal sterna.

Table 10. Descriptive statistics for *E. cupreus* based on 10 males and 10 females from southern Sweden—Skane: Lomma Silvakra. (USNM)

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.93	0.119	0.035	4.1
PW	1.9–2.4	2.10	0.140	0.042	4.4
EL	4.5–5.0	4.81	0.213	0.063	3.0
EW	1.6–1.8	1.76	0.111	0.033	4.2
HW	2.1–2.3	2.22	0.097	0.029	2.9
B. Proportions					
PL/PW	0.843–1.010	0.922	0.054	0.016	3.9
PL/EL	0.383–0.430	0.402	0.018	0.005	3.0
PL/EW	1.030–1.250	1.100	0.077	0.023	4.7
PL/HW	0.814–0.910	0.869	0.040	0.012	3.0
PW/EL	0.408–0.461	0.436	0.020	0.006	3.1
PW/EW	1.130–1.330	1.190	0.065	0.019	3.6
PW/HW	0.893–0.978	0.943	0.039	0.012	2.8
EL/EW	2.650–2.910	2.730	0.094	0.028	2.3
EL/HW	2.070–2.270	2.160	0.065	0.019	2.0
EW/HW	0.711–0.831	0.793	0.040	0.012	3.3

Microsculpture on head, pronotum, elytral intervals 4, 6 and 8, pleura, and thoracic and abdominal sterna subconvex or convex.

*Male genitalia.* Apex of median lobe in lateral view wide and subangular ventro-apically (Fig. 49b); in dorsal view, apex straight, thick-edged (40 microns) and extended far posteriorly from apex of internal sac (Fig. 49a).

*Measurements and proportions.*— Six samples studied, and data for two presented in Tables 10 and 11.

*Variation.*— Specimens from southern Sweden resemble closely those from France, Germany and western Russia (Kaluga near Moscow). Four specimens from arctic Scandinavia are smaller than average. A single specimen east of the Caspian Sea seems typical, though darker. Three specimens from northeastern China differ slightly from European ones. Analysis of ratios suggests the same pattern. Samples of specimens from southern Sweden, Germany and western Russia are similar. Samples from southern Sweden and France are significantly different in the following means: PL/HW, EL/EW and EL/HW. However, the French sample is similar to those from Germany and Russia. Thus gene flow probably exists among these populations. The small sample from arctic Scandinavia consists of small specimens. The sample from northeastern China consists of small specimens with a high ratio PL/EL (0.410). Therefore, I think that gene flow exists between all European populations, and that the slightly modified northeastern Chinese sample may be connected by gene flow with the western Palaearctic samples.

#### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species of the group by restricted meshes of microsculpture on parietale (7% of dorsal surface).

Table 11. Descriptive statistics for *E. cupreus* based on 10 males and 10 females from Marne Region, France.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.0	1.91	0.100	0.030	3.4
PW	2.0–2.2	2.12	0.108	0.032	3.4
EL	4.6–5.1	4.78	0.192	0.059	2.7
EW	1.7–1.9	1.79	0.108	0.032	4.0
HW	2.2–2.4	2.26	0.077	0.023	2.3
B. Proportions					
PL/PW	0.849–0.964	0.904	0.041	0.012	3.0
PL/EL	0.376–0.430	0.400	0.022	0.006	3.6
PL/EW	0.948–1.160	1.070	0.078	0.023	4.9
PL/HW	0.793–0.899	0.840	0.035	0.010	2.8
PW/EL	0.422–0.478	0.443	0.023	0.007	3.4
PW/EW	1.120–1.280	1.180	0.071	0.021	4.0
PW/HW	0.880–0.978	0.930	0.033	0.010	2.3
EL/EW	2.520–2.750	2.670	0.082	0.024	2.0
EL/HW	1.980–2.170	2.100	0.074	0.022	2.3
EW/HW	0.734–0.837	0.786	0.041	0.012	3.5

**Description.**— Seta MP of frontale small. Meshes of microsculpture of parietale narrowly extended (7% of dorsal surface) from constriction behind eye toward occipital suture, and ventrally restricted to constriction behind eye; pointed microsculpture present baso-laterally on 5% of dorsal and ventral surface of parietale. Meshes of microsculpture absent from pronotum, and present on 20% of surface of mesonotum and metanotum; pointed microsculpture present near suture as a narrow band (7% of disc of mesonotum and on 15% of metanotum), restricted laterally (5% of surface of both nota), and absent from posterior band of both nota. Pointed microsculpture indistinctly outlined on urogomphus. Pointed microsculpture of membrane restricted on thorax (20% of ventral surface) and not extended to proepisternum, and present around hypopleuron of abdominal segments 2 to 7.

### Second Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of *E. clairvillei* by lack of meshes of microsculpture on pronotum, and of pointed microsculpture on ventral surface of abdominal membrane near sternites 2 to 7, and from larvae of *E. olivaceous* and *E. laevigatus* by presence of pointed microsculpture near suture of mesonotum and metanotum (2% and 10% of surface respectively), and on lateral portion of both nota (15% of surface).

**Description.**— Pointed microsculpture behind eye restricted (15% of dorsal surface and absent from ventral surface). Meshes of microsculpture absent from disc of pronotum, and present on 40% of surface of mesonotum. Pointed microsculpture near suture of mesonotum and metanotum (2% and 10% of disc respectively), and laterally on both nota (15% of surface). Mesepisternum and metepisternum without microsculpture. Pointed microsculpture on 10% of anterior band of tergum 9. Pointed microsculpture on membrane of abdominal segments 2 to 7 not reaching sternites and extended behind poststernites.

### Third Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of *E. clairvillei* by lack of pointed sculpture near suture of mesonotum, and by restricted development of pointed microsculpture

near suture of metanotum (3% of disc surface), and from larvae of remaining species of the group by pointed microsculpture extended over 60% of anterior band of tergum 9.

**Description.**— Meshes of microsculpture lacking on pronotum, and present on 40% of disc of mesonotum; pointed sculpture lacking near suture of mesonotum, restricted near suture of metanotum (3% of surface), and present laterally on both nota (10% of surface), on 5% of anterior and posterior bands of terga 1 to 8, and on 60% of anterior band of tergum 9. Abdominal sternite 9 with six accessory setae.

### Geographical Distribution and Affinities, and Notes

**Distribution.**— The range of this species extends over most of boreal and cold temperate regions of the Palaearctic Region from the Atlantic coast of Europe (between arctic Scandinavia and Russia in the north, and France, northern Italy, Yugoslavia in the south), east across Siberia to northeastern China (Lindroth, 1945). I have seen specimens from Europe (Norway, Sweden, Finland, Denmark, Russia, Poland, Germany, England, Ireland, Holland, Belgium, France, Switzerland, Austria, Czechoslovakia and Hungary), east of the Caspian Sea (Geoktapa), and from northeastern China (Manchuria). Kryzhanovskij (*in litt.*) reported specimens of this species as far east as the Yakutsk and Lake Baikal regions.

**Collecting notes.**— Adults live on shaded wet organic mud flats where vegetation is scattered or lacking. These mud flats are near small rivers, large lakes, small pools, and in marshy areas of forests. Adults are lacking from pure inorganic soil, but occur on moss, though rarely on *Sphagnum* moss. Populations are known from the alpine zone of Norway and Finland but not from the arctic tundra (Lindroth, 1945:461).

**Taxonomic notes.**— Specimens of this species from northern Scandinavia are darker and match closely the description provided for *E. arcticus*.

I examined 500 adults and dissected six males. I studied three first instar, four second instar and two third instar larvae from Austria.

**Geographical affinities.**— This species is sympatric with *E. sibiricus*, a member of the *cupreus* group, and with *E. uliginosus*, *E. splendidus* and probably with *E. japonicus*, both members of the *uliginosus* group.

### *Elaphrus clairvillei* Kirby

Figs. 50a-b, 73, 76a-g, 80, 82a-b, 85a-c, 90a-b, 96, 98a-c, 111, 122, 133, 160, 162, 163, 164

*Elaphrus clairvillei* Kirby, 1837:61. Type locality: Lake Nipigon, Ontario (restricted by Lindroth, 1961); type (seen by Lindroth) in British Museum (Natural History), London. LeConte, 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Harrington, 1889:139. Blatchley, 1910:48. Hippiusley, 1922:63. Guppy, 1947:51. 1948:76. Clark, 1948:25. Hatch, 1953:63. Lindroth, 1961:112.

*Elaphrus politus* LeConte, 1850:209; Type locality: Maple Island, Ontario (northwest of Sault Ste. Marie); Type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Lindroth, 1961:112.

*Elaphrus frosti* Hippiusley, 1922:64. Type locality: Terrace, British Columbia; type not seen. Lindroth, 1961:112.

*Elaphrus torreyensis* Tanner, 1941:137. Type locality: Torrey, Wayne Co., Utah; type (seen by Lindroth, 1961) in Brigham Young University, Provo, Utah. Lindroth, 1961:112.

*Elaphrus clairvillei* var. *frosti*; Clark, 1948:25. Hatch, 1953:63.

*Elaphrus clairvillei* *lynni* Pierce, 1948b:52. Type locality: Lynne Creek, British Columbia; type (seen by me) in the Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

### Adults

**Diagnostic combination.**— Distinguished from adults of *E. sibiricus* and *E. cupreus* by fused lateral ridges of elytral pits, thus the ridges are ring-shaped (Fig. 133). Distinguished from adults of remaining species by sparse punctures (10 to 120 microns apart) on pleura and

Table 12. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Fawcett, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	2.0–2.1	2.04	0.066	0.020	2.2
PW	2.1–2.3	2.21	0.114	0.034	3.4
EL	4.8–5.5	5.15	0.273	0.081	3.5
EW	1.7–2.0	1.88	0.094	0.028	3.3
HW	2.1–2.3	2.24	0.093	0.028	2.8
<b>B. Proportions</b>					
PL/PW	0.892–0.965	0.928	0.034	0.010	2.5
PL/EL	0.366–0.421	0.397	0.023	0.007	3.8
PL/EW	1.020–1.180	1.090	0.060	0.018	3.7
PL/HW	0.872–0.943	0.913	0.029	0.009	2.1
PW/EL	0.389–0.450	0.428	0.022	0.007	3.5
PW/EW	1.090–1.240	1.180	0.062	0.018	3.5
PW/HW	0.944–1.020	0.984	0.031	0.009	2.1
EL/EW	2.660–2.880	2.750	0.095	0.028	2.3
EL/HW	2.170–2.440	2.300	0.103	0.031	3.0
EW/HW	0.782–0.882	0.838	0.038	0.011	3.0

laterally on thoracic and abdominal sterna.

**Description.**— Upper body surface dark brassy-green or copper (boreal regions and along the Rockies), or darker and even black, elsewhere; pits purple, and postero-lateral angles of pronotum and impression of head bright metallic green in most specimens; ventral body surface black or black with brassy-green hue; legs reddish brown in most specimens from northeastern United States and adjacent areas of Canada, or dark brown, femora with metallic green hue, and dorsal surface of tibiae and tarsomeres purple.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with one pair of submedial impressions. Prosternal process with one to four accessory setae in about 50% of specimens. Metasternum with few punctures antero-medially; most punctures setose. Abdominal sterna 5 and 6 each with 15 to 25 accessory setae, sternum 7 with about 20 in males and five to 15 in females. Setigerous punctures of elytron sharply outlined. Pits of elytron deeply impressed, and with eight to 10 punctures near suture; lateral ridges of pits clearly fused anteriorly and posteriorly (Fig. 133), thus ring-shaped. Mirrors distinct on intervals 3 and 5, and slightly contrasted especially on dark specimens. Femur of foreleg with about 5 setae. Tibia of midleg of males with sharp projection at base of inner spur (Fig. 150). Hind coxa with punctures on outer 0.5 and with three to seven accessory setae near inner margin.

**Integument sculpture.** Punctures 20 to 25 microns in diameter on dorsal body surface, and 25 to 30 microns in diameter on ventral body surface. Punctures 20 to 75 microns apart on lateral portion of pronotum, 30 to 120 microns apart on intervals 4, 6 and 8 (Fig. 122), 50 to 60 microns apart on pleura, 20 to 180 microns apart on prosternum, five to 100 microns apart laterally on abdominal sterna, and 30 to 80 microns apart on coxae.

Meshes of microsculpture outlined in pits and impressions of pronotum very restricted elsewhere on dorsal body surface or not engraved. Microsculpture convex or subconvex on ventral body surface.

**Male genitalia.** Apex of median lobe in lateral view narrow, slightly spatulate, and slightly bent ventrally (Fig. 50b); in dorsal view moderately extended beyond apex of internal sac, thick-edged (40 to 60 microns) and markedly twisted (Fig. 50a).

**Measurements and proportions.**— Twenty-three samples studied, and data for three are presented in Tables 12 to 14.

**Variation.**— The most easily observed variation was color of the dorsal surface (Fig. 162). In northeastern United States and adjacent Canada adults are small, black, with rufous legs. In

Table 13. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Riverton, Manitoba.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.2	2.01	0.109	0.032	3.6
PW	1.9–2.3	2.12	0.138	0.041	4.4
EL	4.6–5.2	4.91	0.269	0.080	3.7
EW	1.6–1.9	1.76	0.114	0.034	4.3
HW	2.1–2.4	2.24	0.100	0.030	3.0
B. Proportions					
PL/PW	0.899–0.988	0.950	0.038	0.011	2.6
PL/EL	0.393–0.433	0.411	0.017	0.005	2.8
PL/EW	1.070–1.220	1.140	0.071	0.021	4.1
PL/HW	0.870–0.933	0.898	0.025	0.007	1.8
PW/EL	0.406–0.448	0.432	0.015	0.005	2.4
PW/EW	1.130–1.280	1.200	0.060	0.018	3.3
PW/HW	0.907–0.989	0.946	0.035	0.010	2.4
EL/EW	2.690–2.900	2.780	0.096	0.028	2.3
EL/HW	2.110–2.310	2.190	0.089	0.027	2.7
EW/HW	0.742–0.844	0.787	0.041	0.012	3.5

western Canada individuals are large, dark green with black legs. This last form also extends southward along the Rocky Mountains to Colorado and eastern Arizona. However, many smooth and dull specimens are mixed among a majority of more typical bright specimens in Utah and Colorado. The Arizona sample includes only dull individuals. The western Canadian form extends into British Columbia and eastern Alaska. West of the continental divide, specimens are darker green than east of there, and those of the Pacific coast are almost black. These data suggest a rather distinct eastern form, a clinal change along the Rocky Mountains from the boreal form to a dull southern form, and a slight differentiation in the Great Basin and Pacific coast regions.

An independent study of body proportions indicates more clearly this same pattern. I carefully chose 23 samples across the range of this species. The most consistent differences were between eastern United States (including adjacent Canada) and the remaining populations. Relative to central and western populations, eastern ones show significantly larger means for the ratios: PL/PW, PL/EL, PL/HW, PW/HW, EL/HW, EW/HW, and significantly smaller means for PL/EW (*i.e.*, eastern specimens have relatively narrower heads, longer pronota and wider elytra. See Figs. 163 and 164). However, some of these differences are less marked northward into southern Manitoba, northern Michigan and on the north shore of the gulf of the St. Lawrence River. The sample from Riverton, Manitoba, is intermediate between eastern and western forms. Thus, the eastern form intergrades with the western form in Manitoba, and probably so across northern Ontario and Quebec, although I have only small samples from that area. Surprisingly, specimens from Newfoundland are typical of the western form. If so, the Newfoundland population might have originated from the western form

Table 14. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Ridgewood, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.1	1.98	0.159	0.036	2.0
PW	2.0–2.2	2.06	0.089	0.026	2.9
EL	4.3–4.9	4.63	0.232	0.069	3.3
EW	1.5–1.8	1.70	0.101	0.030	4.0
HW	2.0–2.3	2.25	0.111	0.033	3.3
B. Proportions					
PL/PW	0.931–1.000	0.963	0.022	0.006	1.5
PL/EL	0.417–0.453	0.428	0.015	0.004	2.3
PL/EW	1.110–1.260	1.170	0.050	0.015	2.8
PL/HW	0.860–0.951	0.882	0.032	0.009	2.4
PW/EL	0.428–0.465	0.445	0.016	0.005	2.4
PW/EW	1.150–1.290	1.210	0.049	0.015	2.7
PW/HW	0.889–1.000	0.916	0.038	0.011	2.8
EL/EW	2.640–2.830	2.730	0.097	0.029	2.4
EL/HW	1.930–2.250	2.060	0.107	0.032	3.4
EW/HW	0.697–0.827	0.755	0.046	0.024	4.1

spreading across Quebec. If not, it may be a relic population. Interpopulational differences in the western form are generally inconsistent. Samples from southern boreal regions (Cypress Hills, Alberta; Churchill, Manitoba; and Newfoundland) and cold grassland (Williams Lake, British Columbia) are similar to those from Colorado and the Great Basin (including the sample from southcentral British Columbia). The sample from eastern Arizona is most similar to that of Colorado, but is consistently different from this and samples of the Great Basin in having a significantly larger mean for ratio PW/HW. The only other significantly different populations are the adjacent samples from southcentral British Columbia and Terrace, British Columbia with those from boreal British Columbia. The first two samples are basically similar to samples south of these localities, but are consistently different from boreal samples with significantly smaller means for ratios PW/HW, EL/HW and EW/HW (*i.e.*, the head is relatively wider). Though these results suggest lack of gene flow between the boreal form and the form south of it, the data on variation suggest gene flow between the Great Basin and Colorado populations and the boreal regions by the Great Basin-Rocky Mountain arc. Samples from western North America (eastern Alaska, northernmost British Columbia, southern Yukon, and northcentral Alberta) show significantly larger means for ratio EW/HW. Most samples also show significantly larger means for ratios PW/HW, EL/HW and PW/EW. These differences are most pronounced in eastern Alaska. Therefore, there is evidence for clinal variation and for gene flow between northwestern populations and other southern and eastern boreal populations.

In summary, I recognize a boreal, a western (Great Basin and Pacific Coast), and a New England (including adjacent Canada) form, but gene flow is apparently uninterrupted between



them. Therefore, I do not consider it necessary to recognize subspecies.

### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of *E. cupreus* by widespread meshes of microsculpture of parietale dorso-laterally (20% of surface), and from larvae of remaining species of the group by lack of microsculpture on the disc of pronotum, and by restricted pointed microsculpture ventrally on thoracic membrane (15% of surface).

*Description.*— Seta MP of frontale small. Meshes of microsculpture of parietale widespread dorso-laterally (20% of surface), and restricted ventro-laterally (2% of surface). Meshes of microsculpture absent from pronotum, and present on 20% of surface of mesonotum and 30% of surface of metanotum; pointed microsculpture moderately restricted near suture (7% of disc of mesonotum and 15% of disc of metanotum), restricted laterally (5% of surface of both nota), and absent from posterior bands of these nota. Pointed microsculpture clearly outlined on urogomphus. Pointed microsculpture of membrane restricted on thorax (20% of ventral surface) and not extended to propisternum, and expanded around hypopleuron of abdominal segments 1 to 8.

### Second Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of *E. cupreus* by presence of meshes of microsculpture on 10% of pronotum, and of pointed microsculpture on membrane reaching abdominal sternites 2 to 7, and from remaining species of the group by presence of pointed microsculpture near suture of mesonotum and metanotum (2%, and 10% of disc respectively), and on anterior band of tergum 9 (10% of band surface).

*Description.*— Pointed microsculpture moderately restricted dorso-laterally (15% of surface), and absent ventro-laterally. Meshes of microsculpture present on 10% of surface of pronotum, on 40% of surface of mesonotum and metanotum. Pointed microsculpture restricted near suture of mesonotum and metanotum (2% and 10% of disc respectively), and laterally on both nota (15% of surface). Mesepisternum and metepisternum without microsculpture. Pointed microsculpture present on 10% of anterior band of tergum 9. Pointed microsculpture of membrane of abdominal segments 2 to 7 reaching sternite and expanded behind poststernites.

### Third Instar Larvae

*Diagnostic combination.*— distinguished from larvae of *E. cupreus* by presence of pointed microsculpture near suture of mesonotum and metanotum (10% of surface), and from other species of the group by presence of pointed microsculpture on lateral portion of mesonotum and metanotum, and on 60% of anterior band of tergum 9.

*Description.*— Meshes of microsculpture lacking on pronotum, and present on 40% of surface of mesonotum; pointed microsculpture present near suture of mesonotum and metanotum (10% of disc), on lateral portion (10% of disc), on 5% or more of anterior and posterior bands of terga 1 to 8, and on 60% of anterior band of tergum 9. Abdominal sternite 9 with six accessory setae.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— The range of this species extends throughout cold temperate and boreal regions of North America, from Alaska to Newfoundland as far north as treeline, and as far south as northern New England in the east and northern California in the west. Along the Rocky Mountains the range of *E. clairvillei* extends south to Colorado and the White Mountains of eastern Arizona (Fig. 160).

*Collecting notes.*— Adults live on soft wet organic mud in the shade of sedges (*Carex* and *Amblystegium* vegetation), or taller vegetation (*Typha* and *Alnus*), or forest canopy. Females oviposit from mid May until late July. Immatures are common in June, and larvae of all three instars can be found together in July. I found pupae in rotten logs. Though development is rapid, teneral adults do not appear until the end of July, thus emergence seems synchronized. Teneral and older adults are seen until the end of September. Thereafter, most adults are found

in forest litter where the soil is naturally well drained, or under bark of old logs that are well above flood level. Only adults overwinter. During the first half of May adults return to marshes. Adults are diurnal and can live for at least two summers (*i.e.*, many females are found in early May with large *corpora lutea*). Larvae live in the same general habitat of adults, but are mostly within soil. Adults are opportunistic feeders, and eat soft-bodied animals. I have not observed predatory behaviour among adults, but larvae attack small arthropods of any type, including each other under laboratory conditions despite abundance of food.

*Taxonomic notes.*— Types of named, conspecific form match typical specimens of population at or near approximate type localities. *E. clairvillei lynni*, a fossil, known from an elytron is a typical adult of *E. clairvillei* as shown by circular ridges around elytral pits, and puncture development in elytral pits and on intervals 4, 6 and 8. This specimen matches extant specimens near the type locality.

I studied more than 1500 adults and dissected more than 100 males. I examined seven first instar, five second instar, and four third instar larvae from George Lake, Alberta.

*Geographical affinities.*— The range of this species overlaps that of *olivaceus*, and perhaps in northeastern California, that of *E. laevigatus*, both members of the *cupreus* group. Its range is also sympatric with those of *E. fuliginosus* and *E. cicatricosus* in eastern North America.

### *Elaphrus olivaceus* LeConte

Frontispiece and Figs. 51a-b, 123, 134, 161, 165, 166, 167

*Elaphrus olivaceus* LeConte, 1863:1. Type locality: Catskill Mountains, New York; type not seen. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Lindroth, 1961:113.

### Adults

*Diagnostic combination.*— Distinguished from adults of other species of this group by brown antennomeres 1 to 3, and by very fine, dense and widespread punctures on metasternum and hind coxae. Otherwise, dorsal body surface similar to that of *E. pyrenoeus* of the *uliginosus* group.

*Description.*— Upper body surface green (bright emerald to olive), blue green, dark brown olive, or reddish brown except for purple pits; ventral body surface dark golden-green or copper; legs, palps and antennomeres 1 to 3 rufous, femora with green or copper hue, apex of tibiae and tarsomeres metallic green or copper on dorsal surface.

Emargination of tooth of mentum 0.2 to 0.25 as deep as length of tooth. Pronotum with two pairs of discal impressions. Prosternal process without accessory setae. Metasternum densely punctate antero-medially; about 20% of punctures with setae. Abdominal sterna 3 and 4 each with 10 to 20 accessory setae, sterna 5, 6 and 7 (in both sexes) each with less than three (Fig. 139). Setigerous punctures on elytron clearly outlined. Elytral pits not deeply impressed, and with eight to 15 punctures; lateral ridges narrow or not distinct, and apparently fused anteriorly and posteriorly (Fig. 134). Mirrors indistinctly outlined on intervals 3 and 5, and weakly contrasted against microsculpture-free intervals 4, 6 and 8. Femur of foreleg with about 20 setae. Tibia of midleg of males without projection at base of inner spur. Hind coxae densely punctate over surface and with two to five accessory setae along inner margins.

*Integument sculpture.* Punctures 15 to 20 microns in diameter on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123), 25 to 30 microns in diameter on pleura, lateral portions of thoracic and abdominal sterna, and on coxae. Punctures 10 to 20 microns apart on head, lateral portion of pronotum, elytral intervals 4, 6 and 8, and on pleura and abdominal sterna, 5 to 50 microns apart on thoracic sterna and coxae.

Meshes of microsculpture absent from head, pronotum (except postero-lateral angles and lateral portion), and elytron (except in pits and near shoulder. See Fig. 134). Microsculpture flat on lateral portion of pronotum, near shoulder, on thoracic sterna, propleuron and mesopleuron; convex or subconvex on metapleuron, abdomen, postero-lateral impressions of pronotum, and elytral pits.

*Male genitalia.* Apex of median lobe in lateral view narrow (Fig. 51b); in dorsal view shortly extended posterior to apex of internal sac, thin-edged (20 microns wide) and straight (Fig. 51a).

*Measurements and proportions.*— Seven samples studied, and data for three are presented in Tables 15 to 17.

Table 15. Descriptive statistics for *E. olivaceus* based on two males and four females from Central Colorado: Fairplay, Santa Maria, Plum Creek, Bellevue.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.6–1.8	1.72	0.087	0.047	3.4
PW	1.8–1.9	1.85	0.050	0.027	1.8
EL	3.8–4.2	4.08	0.215	0.117	3.5
EW	1.4–1.6	1.49	0.117	0.064	5.2
HW	1.9–2.0	1.92	0.050	0.027	1.7
B. Proportions					
PL/PW	0.904–0.973	0.928	0.027	0.020	2.7
PL/EL	0.411–0.429	0.422	0.011	0.006	1.7
PL/EW	1.110–1.200	1.150	0.058	0.031	3.3
PL/HW	0.846–0.936	0.896	0.045	0.024	3.3
PW/EL	0.441–0.474	0.455	0.017	0.009	2.4
PW/EW	1.190–1.330	1.240	0.081	0.044	4.3
PW/HW	0.936–1.000	0.965	0.031	0.017	2.2
EL/EW	2.650–2.810	2.730	0.102	0.055	2.5
EL/HW	1.970–2.210	2.120	0.128	0.069	4.0
EW/HW	0.705–0.813	0.779	0.064	0.035	5.5

*Variation.*— Adults from Colorado, Alberta and eastern North America, at first glance, are similar. However, populations from these regions differ in the number of different color forms (see Fig. 165). In coastal New England there are two color forms: blue-green and olive. In interior New England (*i.e.*, Green Mountains, Vermont and Adirondack Mountains, New York) these two forms co-exist with a third dark brown form with green punctures. This last form is not discrete because specimens between this and the olive form exist. In boreal Québec, on the north shore of the St. Lawrence River (St. Fidèle), the brown form with golden punctures is discrete. From this last locality to Medicine Hat, Alberta, I have seen specimens of these three color forms. Westward the brown form with golden punctures turns reddish brown. In central and northern Alberta, I collected only two color forms: olive and red-brown. This last form has copper punctures. From Newfoundland I have two forms: olive and blue-green, and from Colorado only olive specimens. However, these two samples are too small to determine the range of color forms. These results suggest a cline from east to west in the formation and differentiation of a third color form. Three forms exist from eastern Canada to Medicine Hat, Alberta, but only two in central Alberta. Thus, there is a suggestion of a break in gene flow, but the reddish-brown form, though distinct, is nevertheless most similar to the brown form from Medicine Hat. Therefore, gene flow might still exist in areas of either the Rocky Mountain foothills or the boreal regions of Saskatchewan and Manitoba that have not been adequately sampled.

In an attempt to clarify this problem, I studied variation in body proportions of adults of carefully chosen samples from across the range of this species. Results confirmed and completed the general picture presented above. The Colorado sample showed the lowest mean

Table 16. Descriptive statistics for *E. olivaceus* based on 10 males and 10 females from Flatbush, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.81	0.108	0.032	4.0
PW	1.7–2.0	1.83	0.111	0.033	4.0
EL	4.0–4.6	4.23	0.266	0.079	4.2
EW	1.4–1.7	1.55	0.134	0.040	5.7
HW	1.8–2.1	1.93	0.091	0.027	3.1
B. Proportions					
PL/PW	0.946–1.040	0.993	0.047	0.014	3.2
PL/EL	0.403–0.455	0.430	0.023	0.007	3.6
PL/EW	1.070–1.290	1.170	0.080	0.024	4.6
PL/HW	0.900–0.974	0.937	0.034	0.010	2.4
PW/EL	0.407–0.462	0.433	0.022	0.007	3.4
PW/EW	1.090–1.260	1.180	0.073	0.022	4.2
PW/HW	0.909–1.000	0.944	0.073	0.010	2.4
EL/EW	2.580–2.860	2.720	0.100	0.030	2.4
EL/HW	2.100–2.290	2.180	0.083	0.025	2.5
EW/HW	0.747–0.857	0.813	0.046	0.014	3.8

values for ratios PL/PW and PL/EL (*i.e.*, the pronotum is relatively short. See Fig. 166). This sample is most similar to that of central Alberta, and most different from that of Medicine Hat, Alberta. The central Alberta sample is consistently different from all more eastern samples with its significantly larger mean for ratio EL/HW. It also differs significantly from most eastern samples in its mean for each of the following ratios: PL/HW, PW/HW and EW/HW (*i.e.*, the head is relatively narrower. See Fig. 167). The central Alberta sample is most similar to that of Medicine Hat, and increasingly different from samples eastward. The sample from a locality east of Medicine Hat most similar to the western samples is from southern Manitoba, and the most different samples are those from New Brunswick and Newfoundland. The progressively more extensive differentiation of the Medicine Hat sample from more easterly samples suggests gene flow between eastern and western complexes, and among the latter samples. Samples of the eastern complex (Manitoba to Newfoundland) are generally similar to one another in the features studied.

The data suggest basically three forms: one from Colorado, another from northern Alberta, and a third extending from Medicine Hat, Alberta, eastward. However, the Medicine Hat sample is both most proximate and most similar to the Colorado and Northern Alberta samples. Although more specimens are needed from the Rocky Mountain area and the northern Prairie provinces, the data suggest that gene flow takes place among these populations. Therefore, I do not consider it appropriate to recognize subspecies.

Table 17. Descriptive statistics for *E. olivaceus* based on 11 males and 9 females from Medicine Hat, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.7–2.0	1.82	0.145	0.043	5.3
PW	1.7–2.0	1.87	0.144	0.043	5.1
EL	3.6–4.6	4.17	0.387	0.115	6.2
EW	1.3–1.7	1.53	0.159	0.047	6.9
HW	1.7–2.1	1.96	0.126	0.037	4.3
<b>B. Proportions</b>					
PL/PW	0.921–1.030	0.975	0.034	0.010	2.3
PL/EL	0.415–0.479	0.439	0.022	0.006	3.3
PL/EW	1.120–1.270	1.190	0.061	0.018	3.4
PL/HW	0.875–0.964	0.929	0.039	0.011	2.8
PW/EL	0.425–0.500	0.450	0.026	0.008	3.8
PW/EW	1.150–1.330	1.220	0.066	0.020	3.6
PW/HW	0.913–1.000	0.951	0.042	0.013	3.0
EL/EW	2.640–2.830	2.710	0.076	0.023	1.9
EL/HW	1.900–2.260	2.120	0.115	0.034	3.6
EW/HW	0.714–0.840	0.781	0.044	0.013	3.7

**First Instar Larvae**

*Diagnostic combination.*— Distinguished from larvae of *E. laevigatus* by restricted pointed microsculpture on parietale behind eye (5% of dorsal and 3% of ventral surfaces), and from larvae of remaining species of the group by the presence of meshes of microsculpture on pronotum (5% of surface), by the extended pointed microsculpture on ventral surface of thoracic membrane (45% of surface), by the very fine pointed microsculpture of urogomphi, and by the restricted pointed microsculpture on the base of abdominal sternite 10.

*Description.*— Seta MP of frontale very small. Meshes of microsculpture of parietale expanded baso-laterally (50% of dorsal surface) and ventro-laterally; pointed microsculpture restricted to constriction behind eye (5% of dorsal surface and 3% of ventral surface). Meshes of microsculpture present on 5% of disc of pronotum, and on 40% of surface of mesonotum and metanotum; pointed microsculpture of mesonotum and metanotum widespread near suture (20% of surface), restricted laterally (5% of surface), and absent from posterior band. Pointed microsculpture clearly outlined on urogomphus. Pointed microsculpture of membrane expanded on thorax (40% of surface), and extended to proepisternum, and extended around hypopleuron of abdominal segments 2 to 7.

**Second Instar Larvae**

*Diagnostic combination.*— Distinguished from larvae of *E. laevigatus* by the restricted pointed microsculpture behind eye (15% of dorsal and 3% of ventral surface of parietale). Distinguished from larvae of remaining species of the group by lack of pointed microsculpture from mesonotum and metanotum, and from the anterior band of tergum 9.

*Description.*— Pointed microsculpture behind eye restricted (15% of dorsal surface and 3% of ventral surface of parietale). Meshes of microsculpture present on 30% of surface of pronotum, and on 40% of surface of mesonotum. Pointed microsculpture absent from mesonotum and metanotum. Mesepisternum and metepisternum without sculpture. Pointed microsculpture absent from anterior band of tergum 9. Pointed microsculpture of abdominal membrane extended around

hypopleura and behind poststernites.

### Third Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of *E. laevigatus* by presence of meshes of microsculpture on 10% of disc of pronotum, and on 40% of disc of mesonotum and metanotum, and from those of remaining species of the group by absence of pointed microsculpture from mesonotum and metanotum, and anterior band of tergum 9.

*Description.*— Meshes of microsculpture present on 10% of pronotum and 40% of surface of mesonotum and metanotum; pointed microsculpture absent from nota, anterior band of tergum 9, and posterior band of terga 1 to 8. Abdominal sternite 9 with two accessory setae.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— The range of this species extends across the southern boreal and cold temperate regions of North America, from central British Columbia to Newfoundland south to New Jersey and along the Rocky Mountains to Colorado (Fig. 161).

*Collecting notes.*— Adults live on soft or firm organic mud flats exposed to sunlight. In Massachusetts these beetles were common in *Typha* marshes on sun-exposed ground. On the north shore of the St. Lawrence River I found many specimens on firm brown mud among scattered clumps of *Carex nigra*. In Gatineau Park, Quebec, I found them on the fine soft muds of an abandoned beaver pond. In Alberta, adults and larvae are commonly obtained from *Carex* swamps near the *Typha* zone where clumps of *Carex rostrata* are sparser, and where thin brown mosses are found above water. An excellent method to concentrate these beetles was to cultivate the *Carex* zone into a clean black organic mud flat. This heliophilous species has a life cycle similar to that of *E. clairvillei*. However, I do not know where adults of *E. olivaceus* overwinter.

*Taxonomic notes.*— I have examined about 1100 adults and dissected 10 males. I studied five first instar, two second instar, and 10 third instar larvae from George Lake, Alberta.

*Geographical affinities.*— This species occurs sympatrically with *E. clairvillei*, a member of the *cupreus* group, and also with *E. fuliginosus* and *E. cicatricosus*, both members of the *fuliginosus* group.

### *Elaphrus laevigatus* LeConte

Figs. 52a-b, 161

*Elaphrus laevigatus* LeConte, 1852:200. Type locality: San Francisco, California; type (seen by me) in the Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:5. Blatchley, 1910:48. Van Dyke, 1925:113. La Rivers, 1946:138. Hatch, 1953:63 Lindroth, 1961:113.

*Elaphrus politus* Casey, 1897:345 (junior homonym of *E. politus* LeConte, 1850). Type locality: San Francisco, California; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington. D.C. Van Dyke, 1925:113. Lindroth, 1961:113.

*Elaphrus caseyi* Leng, 1918:203. New name for the junior homonym proposed by Casey, 1897.

### Adults

*Diagnostic combination.*— Distinguished from specimens of other species of this group by sparse dorsal punctures (10 to 200 microns apart), and by dense ventral punctures on pleura (5 to 20 microns apart).

*Description.*— Upper body surface black except for blue-green postero-lateral impressions of pronotum, pits and punctures; ventral surface black with faint metallic golden-green hue; legs and palpi piceous, femora with metallic blue-green hue, and dorsal surface of tibia and tarsomeres with metallic purple hue.

Table 18. Descriptive statistics for *E. laevigatus* based on 10 males and 10 females from San Francisco Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.6–1.8	1.71	0.098	0.029	3.8
PW	1.8–2.0	1.89	0.116	0.035	4.1
EL	3.9–4.4	4.14	0.240	0.071	3.9
EW	1.3–1.6	1.46	0.115	0.034	5.3
HW	1.7–2.0	1.89	0.113	0.034	4.0
<b>B. Proportions</b>					
PL/PW	0.868–0.973	0.905	0.040	0.012	2.9
PL/EL	0.400–0.450	0.414	0.017	0.005	2.8
PL/EW	1.110–1.330	1.180	0.074	0.022	4.2
PL/HW	0.875–0.960	0.907	0.032	0.009	2.3
PW/EL	0.439–0.475	0.458	0.012	0.003	1.7
PW/EW	1.250–1.410	1.300	0.058	0.017	3.0
PW/HW	0.973–1.060	1.000	0.034	0.010	2.2
EL/EW	2.750–2.960	2.840	0.090	0.027	2.1
EL/HW	2.120–2.290	2.190	0.073	0.022	2.2
EW/HW	0.720–0.797	0.772	0.032	0.010	2.8

Emargination of tooth of mentum half as deep as length of tooth. Pronotum with one pair of submedial impression. Intercoxal process of prosternum without accessory setae. Antero-medial surface of metasternum with few punctures; most punctures with setae. Abdominal sterna 5 and 6 with about 10 accessory setae, sternum 7 in males with 10 to 20 setae and in females with about five. Setigerous punctures of elytron indistinctly outlined. Pits of elytra deeply impressed, and with four or five punctures; lateral ridges of pits wide and fused anteriorly and posteriorly. Mirrors indistinctly outlined and not contrasted against brilliant intervals 4, 6 and 8. Femur of foreleg and midleg with about 40 setae. Tibia of midleg of males without projection at base of inner spur. Hind coxae with few outer punctures and three to five accessory setae near inner margin.

*Integument sculpture.* Punctures 10 to 25 microns in diameter on clypeus, head, pronotum, on elytral intervals 4, 6 and 8, and on coxae; 25 to 30 microns in diameter on pleura and lateral portions of thoracic and abdominal sterna. Punctures 10 to 200 microns apart on pronotum, about 60 microns apart at base of head, five to 20 microns apart on pleura, and 25 to 100 microns apart on lateral portion of thoracic and abdominal sterna.

Microsculpture flat in postero-lateral impressions of pronotum and in elytral pits, absent from most of dorsal body surface, flat ventrally.

*Male genitalia.* Apex of median lobe in lateral view moderately widened near internal sac. (Fig. 2); in dorsal view apex shortly extended posterior to base of internal sac, thin-edged (20 microns wide) and straight (Fig. 52a).

*Measurements and proportions.*— Two samples studied, with one presented in Table 18.

*Variation.*— A sample from localities near San Francisco shows smaller means for measurements than that from northeastern California. Specimens from northeastern California have relatively wide elytra (ratios: EL/EW = 2.73, and EW/HW = 0.805).

### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of *E. olivaceus* by widespread microsculpture on baso-lateral portion of parietale (50% of dorsal surface and 15% of ventral surface), and from larvae of other species by presence of meshes of microsculpture on the pronotum.

**Description.**— Seta MP of frontale very small. Pointed microsculpture widespread laterally on parietale (50% of dorsal surface and 15% of ventral surface). Meshes of microsculpture present on 10% of surface of pronotum, and on 50% of surface of mesonotum; pointed microsculpture of mesonotum and metanotum moderately widespread near suture (10% of disc), widespread laterally (35% of disc), and on 60% of surface of posterior band. Pointed microsculpture of urogomphus distinctly outlined. Pointed microsculpture of membrane moderately widespread on thorax (30% of ventral surface) and clearly extended to proepisternum, and restricted on abdomen to epipleura.

## Second and Third Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of *E. olivaceus* by widespread microsculpture on parietale especially behind eye (50% of dorsal surface and 10% of ventral surface), and from larvae of remaining species of the group by absence of pointed microsculpture near suture of mesonotum and metanotum, and from anterior band of tergum 9.

## Second Instar Larvae

**Description.**— Pointed microsculpture of parietale widespread baso-laterally (30% of dorsal surface and 5% of ventral surface). Meshes of microsculpture on 75% of surface of pronotum, on 90 to 100% of surface of mesonotum. Pointed microsculpture present laterally on mesonotum (10% of surface) and absent near suture. Mesepisternum and metepisternum with fine multi-pointed microsculpture. Pointed microsculpture absent from anterior band of tergum 9. Pointed microsculpture of abdominal membrane not extended around hypopleuron.

## Third Instar Larvae

**Description.**— Meshes of microsculpture present on 75% of surface of pronotum, and 90 to 100% of surface of mesonotum; pointed microsculpture absent from lateral portion of mesonotum and metanotum, present on 5% or more of anterior band of terga 1 to 8, absent from posterior band of terga 1 to 8 and anterior band of tergum 9. Abdominal sternite 9 with two accessory setae.

## Geographical Distribution and Affinities, and Notes

**Distribution.**— The range of this species extends from northern California as far south as Los Angeles area, and as far east as Reno, Nevada (Fig. 161).

United States. CALIFORNIA (4;ANSP, UMRM, DEFW, AMNH): Hullville (2;MCZC); Alameda Co. (3;KSUC, FMNH); Oakland (1;CASC); Fresno Co., Fresno (1;ICCM); Kern Co., Mill Portrero (1;LACM); Lassen Co., Norvell--misspelled Norval (1;CASC); Warner Valley, Lassen National Forest (1;CASC); Los Angeles Co., Claremont (1;CUIC); Madera Co., Chiquito Creek, 4100' (2;CUIC, USNM); North Fork--misspelled Northfork (3;CUIC, USNM); Marin Co., Inverness (1;CASC), Tamales Bay (1;CASC); Monterey Co., Carmel (3;CASC, UASM), Monterey (2;CASC); Plumas Co., 6 mi. n.w. Chester (1;USNM); 4 mi. w. Quincy (1;UCRC); San Francisco Co., (42;USNM, CASC, MCZC, SEMC), San Francisco (22;USNM, CASC, ANSP, PURC); San Luis Obispo Co., San Luis Obispo (1;FMNH); Sonoma Co., Eldridge (1;CASC); Siskiyou Co., (2;CASC); Trinity Co., Carrville (5;CASC); Tuolumne Co., (1;CASC). NEVADA: Washoe Co., Reno (1;MCZC). NEW YORK: Barre-- no doubt mislabelled (1;CUIC).

**Collecting notes.**— Adults of this species live on soft black mud under dead and dense *Juncus*-like vegetation. This habitat is in the shade of deciduous and broad-leaf evergreen trees during the day, and is similar to that described for *E. clairvillei*. Oviposition took place in the laboratory soon after obtaining adults in April. I saw a teneral adult collected in late September in Warner Valley, Lassen Co., therefore, in northeastern California populations probably overwinter as adults.

**Taxonomic notes.**— I examined 130 adults and dissected 4 males. I studied six first instar, five second instar, and five third instar larvae from San Francisco, California.

**Geographical affinities.**— Allopatric, but probably sympatric in northeastern California with *E. clairvillei*, a member of the *cupreus* group.

## Subgenus *Elaphrus* Fabricius

*Elaphrus* Fabricius, 1775:227. Type-species: *Cicindela riparia* Linnaeus, 1758, fixed by Latreille (1810), by subsequent



designation, Hatch, 1951:113. 1953:63; Ball, 1960:106. Lindroth, 1961:114. Nakane *et al.*, 1963: 19.

*Elaphroterus* Semenov, 1895:309. 1904a:19. Jacobson, 1906:267. Reitter, 1908:96;97. 1909:104. Bänninger, 1919:149. Porta, 1923:78. Portevin, 1929:41. All *ex parte*.

*Trichelaphrus* Semenov, 1926:39. Type-species: *Cicindela riparia* Linnaeus, 1758, fixed by Semenov, (1926), by original designation. Bänninger, 1931:184. Jeannel, 1941:216.

## Adults

**Diagnostic combination.**— Distinguished from adults of other subgenera as in following. Clypeus with two pair of setae. Trochanter of foreleg and midleg with three setae. Setae covering hind coxa. Process of mesosternum setose.

**Description.**— *Head.* Frons without medial impression (though suggested by elongate punctures and by irregular carinae). Clypeus with two pairs of setae. Terebral margin of right mandible more than 0.5 of mandible length; basal tooth of retinaculum entire, and apex of retinacular tooth near terebral tooth (Fig. 4).

*Thorax.* Lateral margin of pronotum beaded except in situation (completely beaded in adults of *E. marginicollis*). Fringe of setae along posterior margin of pronotum reaching hind angles; setae of fringe scimitar-shaped and enlarged apically. Proepimeron and proepisternum apparently fused. Prosternum setose. Process of mesosternum setose; postero-lateral ridge of mesosternum absent.

*Abdomen.* Tergum 7 without setae except on stridulatory scrapers.

*Elytra.* Striae lacking. Transverse basal stria slightly expressed at shoulder. Setigerous punctures of elytron 40 to 50 microns in diameter. First sutural mirror wide, others narrower (except in some individuals of *E. viridis*). Elytral pits with 50 to 200 regularly distributed punctures (Figs. 20 to 25).

*Legs.* Foreleg: trochanter with three setae; femur with 60 to 85 setae; tibia with 25 to 45 setae; inner dorsal fringe 0.7 to 0.75 as long as tibia, and without setae posteriorly; first three tarsomeres of males with ventral spongy pubescence. Midleg: trochanter with three setae; femur with 60 to 95 setae; tibia with 65 to 115 setae. Hindleg: coxa with setae covering surface; femur with 24 to 31 setae; tibia with 70 to 95 setae.

*Male genitalia.* Internal sac of median lobe without scales posteriorly.

*Ovipositor.* Basal sclerite of stylus without apico-ventral setae; apical sclerite with two to six lateral stout setae on dorso-medial and dorso-lateral ridges, apex without setae (Fig. 75).

## All Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of other subgenera as in following. Seta EA-E on frontale very small. Epicranial suture small, less than 0.7 length of antennal scape. Outer surface of stipes with membranous declivity behind postero-lateral seta, outer margin straight; postero-lateral pores proximate (Fig. 83b).

## First Instar Larvae

**Description.**— Medial point of nasale acute; teeth of nasale absent or extremely fine, and ending at base of medial point (Fig. 91). Setae Ea-E of parietale very small. Epicranial suture less than 0.7 as long as antennal scape. Head short; bisinuation of lateral margin behind eye with anterior and posterior convexity subequal. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 90° to 110°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale short (anterior angle open). Pointed microsculpture absent from ventral surface of parietale. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin straight (Fig. 83b); dorsal surface with about 30 setae on inner half, subapical setae roughly distributed in two rows; postero-ventral pores proximate (Fig. 83b). Pronotum covered with meshed microsculpture, pointed microsculpture present on 3 to 5% of surface. Pointed microsculpture absent from surface of anterior band of terga 1 to 8.

## Second Instar Larvae

**Description.**— Outer margin of stipes behind postero-lateral seta projected outward. Each sclerite of pronotum and mesonotum with about 15, and eight to 10 accessory setae respectively; pointed microsculpture present on 30 to 40% of anterior band of mesonotum. Each sclerite of terga 1 to 8 with seven to nine accessory setae. Basal major accessory seta of urogomphus near middle; pointed sculpture present on entire band surface of terga 1 to 9, and on entire posterior band of terga 1 to 8. Hypopleuron of segments 1 to 8 with about four accessory setae.

### Third Instar Larvae

*Description.*— Each sclerite of mesonotum with 23 to 25 accessory setae, and mesonotal epipleuron with one accessory seta. Mesepimeron with fewer than three accessory pores. Largest projection of urogomphus in lateral view large (Fig. 100b). Sclerite of terga 1 to 8 each with 17 to 20 accessory setae. Epipleuron of abdominal segments 2 to 8 with eight to 14 accessory setae. Hypopleuron of abdominal segment 1 to 8 with eight to 10 accessory setae. Sternite of abdominal segment 1 with four to eight accessory setae, those of segments 2 to 7 each with 12 to 20, that of segment 8 with 14 to 20, that of segment 9 without or up to four, and that of segment 10 with five or less. Inner poststernites each with one to two accessory setae.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— The range of species of this subgenus extends across Palaearctic and Nearctic Regions, from the southern edge of the tundra to the southern edge of the warm temperate Zone.

### Key to the species of subgenus *Elaphrus* Fabricius

#### Adults

- 1 Lateral margin of pronotum clearly beaded in sinuation (Fig. 20). Puncture 40 to 50 microns in diameter on pronotum, and 25 microns in diameter on elytra. Western Nearctic Region ..... *E. marginicollis* new species p. 288
- 1' Lateral margin of pronotum not beaded in sinuation (Figs. 21 and 25). Puncture 20 to 30 microns in diameter on pronotum and elytra ..... 2
- 2 (1') Lateral margin of pronotum explanate near middle and projected (best seen in lateral view) (Figs. 77a, 77b, 77c). Punctures of pronotum almost as dense submedially as antero-laterally. Main mirror near suture roughly ovate (Figs. 114, 115, 126 and 127) ..... 3
- 2' Lateral margin of pronotum not explanate near middle and not projected (Fig. 77d). Punctures of pronotum twice as dense submedially as antero-laterally. Main mirror of most specimens rectangular (Figs. 116, 117, 128 and 129) ..... 5
- 3 (2) Elytral pits large: intervals 4, 6 and 8 almost absent and much disrupted (Figs. 115 and 127). Accessory setae present on pronotum only (Fig. 105). Pronotum with many impressions on disc (Fig. 105). Frons with medial impression. Morocco and Spain ..... *E. lheritieri* Antoine p. 290
- 3' Elytral pits absent (Figs. 114 and 126) or relatively small: intervals 4, 6 and 8 wide and almost straight (Figs. 116 and 128). Accessory setae present on head and pronotum (Fig. 105). Pronotum not impressed except near hind angle (Fig. 106). Frons without medial impression. California ..... 4
- 4 (3') Elytral pits absent (Figs. 114 and 126). Punctures of dorsal surface 5 to 10 microns apart. Accessory setae abundant and long on head and pronotum (Fig. 106). Accessory setae on at least abdominal sternum 5 extended laterally to punctate area (Figs. 143 and 144). Dorsal surface brilliant metallic green ..... *E. viridis* Horn p. 291
- 4' Elytral pits clearly developed (Figs. 116 and 128). Punctures of pronotum 10 to 20 microns apart. Accessory setae sparse and short on head and pronotum. Accessory setae on abdominal sterna not extended laterally to

- punctate area (Fig. 140). Dorsal surface dark green ..... *E. mimus* new species p. 290
- 5 (2') Abdominal accessory setae extended at least to edge of fifth sternum (Figs. 141 to 144) ..... 11
- 5' Abdominal accessory setae not extended to edge of sterna -- on most specimens between ambulatory setae and punctate area (Fig. 140) ..... 6
- 6 (5') Punctures of proepisternum 20 to 40 microns apart (Fig. 109). Third visible sternum with 40 to 60 punctures on each side (Fig. 141). Males and females with similar abundance of accessory setae on abdominal sterna ..... 7
- 6' Punctures of proepisternum 10 to 25 microns apart. Abdominal sternum 3 with 100 to 200 punctures on each side (Fig. 140). Most females with fewer accessory setae on abdominal sterna than males. Nearctic Region ..... 8
- 7 (6) Punctures on proepisternum large (50 to 60 microns in diameter), surface around them depressed (Fig. 109); surface of proepisternum almost black: microsculptured surfaces dark copper and punctures dark blue-green. Eastern Nearctic Region ..... *E. ruscarius* Say p. 293
- 7' Punctures of proepisternum 30 to 40 microns in diameter, surface around them barely or not depressed; surface of proepisternum metallic: microsculptured surfaces copper and punctures green. Western China or adjacent U.S.S.R. .... *E. hypocrita* Semenov p. 293
- 8 (6') Pronotum enlarged at middle (Fig. 24); anterior transverse impression sharply impressed toward antero-lateral angle. Antennomere 3 with 30 to 40 setae (Fig. 13) -- most setae on posterior surface. Prairie regions of Nearctic Region ..... *E. lecontei* Crotch p. 295
- 8' Pronotum slightly enlarged at middle (Fig. 25); anterior transverse impression not impressed. Antennomere 3 without or with less than 20 accessory setae (Figs. 11, 12) ..... 9
- 9 (8) Hind femur, dorsal aspect with three to seven long (100 to 150 microns) white setae subapically (Fig. 35). Elytra strongly constricted in basal 0.3 -- less evident in females. Nearctic Region ..... *E. californicus* Mannerheim p. 299
- 9' Hind femur, dorsal aspect with one (rarely two or three) short (40 to 80 microns) white setae subapically (Fig. 34). Elytra slightly constricted in basal 0.3 ..... 10
- 10 (9') Median lobe of males long: distance between ventral angular bend and apex, in lateral view, 4.6 to 5.3 mm; apex, in lateral view, wide (Fig. 66b), and in ventral view, thin-edged (10 microns) and twisted (Fig. 66a). From southern Oregon, southern Idaho, southwestern Montana and southward ..... *E. finitimus* Casey p. 303
- 10' Median lobe of males short: distance between ventral angular bend and apex, in lateral view, 3.5 to 4.7 mm; apex in lateral view, wide (south of central British Columbia and southwestern Alberta) or narrow, and, in ventral view, thick-edged (35 microns), slightly twisted (south of central British Columbia and southwestern Alberta) or straight (Figs. 67a, 68a and 69a). North of central Oregon, central Idaho and Colorado, and east of these regions in forested areas ..... *E. americanus* Dejean p. 307

- 11 (5) Hind femur, in dorsal view, with three to seven long (about 150 microns) white setae subapically (Fig. 35). Apex of median lobe of males truncated (Fig. 63b). Specimen from northeastern China or Japan ..... *E. comatus* new species p. 311
- 11' Hind femur, in dorsal view, with one to three small (40 to 80 microns) white setae subapically (Fig. 34). Apex of median lobe rounded (Fig. 61a) ... 12
- 12 (11') Abdominal sternum 3 with less than 40 punctures laterally (Fig. 142). Punctures in pits separated by two to four rows of meshes of microsculpture (Fig. 136) ..... 14
- 12' Abdominal sternum 3 with 40 to 80 punctures laterally (Fig. 141). Punctures in pits separated by one to three rows of meshes of microsculpture ..... 13
- 13 (12') Microsculpture scale-like (best seen with diffused light) on abdominal sterna between ambulatory setae and edge of sternum (Figs. 143 and 153). Antennomere 3 without accessory seta. Elytron with one row of sharply delineated mirrors in most specimens (Fig. 117). Tibia of foreleg mostly red-brown except for metallic apex and base. Boreal and temperate Palaearctic Region ..... *E. riparius* (Linnaeus) p. 313
- 13' Microsculpture on abdominal sterna flat or subconvex--scale-like in some specimens of *E. tuberculatus* (Fig. 144). Antennomere 3, in most specimens, with some accessory setae. Elytron with two or three rows of sharply delineated mirrors in most specimens (Fig. 116). Tibia of foreleg of most specimens mostly or entirely metallic. Arctic and subarctic regions of Palaearctic and western Nearctic Regions ..... *E. tuberculatus* Mäklin p. 316
- 14 (12) Punctures 20 microns in diameter on elytral pits, and 25 microns on pronotum. Pronotum with long sinuation along lateral margin. Specimen from eastern Tibet, China ..... *E. tibetanus* Semenov p. 320
- 14' Punctures of elytral pits and pronotum 25 to 30 microns in diameter. Pronotum with short sinuation along lateral margin. Tundra regions of western Nearctic Region and Commander Islands, U.S.S.R. .... *E. parviceps* Van Dyke p. 319

### First Instar Larvae

- 1 Antero-dorsal seta of abdominal epipleura 2 to 5 and 8 sub-equal and very small. Epicranial suture 0.2 to 0.3 as long as antennomere 1. Apical inner margin of mandible smooth, posterior margin of retinaculum toothed. Nearctic Region ..... *E. californicus* Mannerheim p. 299
- 1' Antero-dorsal seta of abdominal epipleura 2 to 5 small and much larger than that of epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1. Apical inner margin of mandible toothed, if smooth, then posterior margin of retinaculum also smooth ..... 2
- 2 (1') Seta PII-P of nota about 20 microns in length, only slightly larger than that of terga. Seta VEM-P on parietale very small. Prairie regions of Nearctic Region ..... *E. lecontei* Crotch p. 295

- 2' Seta PII-P of nota about 40 microns in length, about twice as long as that of terga. Seta VEM-P of parietale small ..... 3
- 3 (2') Antero-dorsal seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region .....  
..... *E. ruscarius* Say p. 293
- 3' Antero-dorsal seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 ..... 4
- 4 (3') Apical inner margin of mandible and posterior margin of retinaculum smooth. Temperate or boreal Palaearctic Region .....  
..... *E. riparius* (Linnaeus) p. 313
- 4' Apical inner margin of mandible and posterior margin of retinaculum clearly toothed ..... 5
- 5 (4') Seta AIM much smaller on tergum 8 than that of terga 1 to 5. Nearctic Region ..... *E. americanus* Dejean p. 307
- 5' Seta AIM as large on tergum 8 as that of terga 1 to 5. Western Nearctic Region ..... *E. tuberculatus* Mäklin p. 316

## Second Instar Larvae

- 1 Antero-dorsal basic seta of abdominal epipleura 2 to 5 and 8 subequal and very small. Epicranial suture less than 0.3 as long as antennomere 1. Nearctic Region ..... *E. californicus* Mannerheim p. 299
- 1' Antero-dorsal basic seta of abdominal epipleura 2 to 5 small yet much larger than same seta on epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1 ..... 2
- 2 (1') Seta PII-P of nota 10 to 20 microns in length, and subequal to that of terga. Seta VEM-P of parietale very small in most specimens. Prairie region of Nearctic Region ..... *E. lecontei* Crotch p. 295
- 2' Seta PII-P of nota moderately 40 to 60 microns in length, about twice as long as that of terga. Seta VEM-P of parietale small ..... 3
- 3 (2') Antero-dorsal basic seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region .....  
..... *E. ruscarius* Say p. 293
- 3' Antero-dorsal basic seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 ..... 4
- 4 (3') Tergum 9 with dark brown urogomphus. Seta AII and AIM of nota small. Temperate or boreal Palaearctic Region .... *E. riparius* (Linnaeus) p. 313
- 4' Tergum 9 with straw colored urogomphus. Seta AII and AIM of nota medium-sized to large ..... 5
- 5 (4') Seta AIM as large on tergum 8 as that of tergum 1 to 5. Northwestern Nearctic Region ..... *E. tuberculatus* Mäklin p. 316
- 5' Seta AIM much smaller on tergum 8 than that of terga 1 to 5. Nearctic Region ..... *E. americanus* Dejean p. 307

## Third Instar Larvae

- |        |  |  |   |
|--------|--|--|---|
| 1      | Antero-dorsal basic seta of abdominal epipleura 2 to 5 and 8 subequal and very small. Epicranial suture less than 0.3 as long as antennomere 1. Nearctic Region . . . . .                        | <i>E. californicus</i> Mannerheim p. 299 |   |
| 1'     | Antero-dorsal basic seta of abdominal epipleura 2 to 5 small yet larger than that of epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1 . . . . .                               |  | 2 |
| 2 (1') | Parietale much paler at base than elsewhere; pronotum pale in lateral 0.3. Seta PII-P of nota 10 to 20 microns in length, subequal to that on terga. Prairie region of Nearctic Region . . . . . | <i>E. lecontei</i> Crotch p. 295         |   |
| 2'     | Parietale dark or as pale as behind eyes; pronotum dark brown. Seta PII-P of nota 40 to 80 microns in length, and about twice as long as that of terga . . . . .                                 |  | 3 |
| 3 (2') | Antero-dorsal basic seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region . . . . .   | <i>E. ruscarius</i> Say p. 293           |   |
| 3'     | Antero-dorsal basic seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 . . . . .  |  | 4 |
| 4 (3') | Tergum 9 with dark brown urogomphus. Seta AII and AIM of nota small. Temperate or boreal Palaearctic Region . . . . .  | <i>E. riparius</i> (Linnaeus) p. 313     |   |
| 4'     | Tergum 9 with straw colored urogomphus. Seta AII and AIM of nota medium-sized to large . . . . .   |  | 5 |
| 5 (4') | Seta AIM as large on tergum 8 as that of terga 1 to 5. Northwestern Nearctic Region . . . . .  | <i>E. tuberculatus</i> Mäklin p. 316     |   |
| 5'     | Seta AIM much smaller on tergum 8 than that of terga 1 to 5 . . . . .  |  | 6 |
| 6 (5') | Pointed microsculpture absent from anterior and present laterally on 50% of posterior bands of terga 2 to 8. Western Nearctic Region . . . . .   | <i>E. finitimus</i> Casey p. 303         |   |
| 6'     | Pointed microsculpture present on entire anterior and posterior bands of terga 2 to 8. Forested regions of Nearctic . . . . .  | <i>E. americanus</i> Dejean p. 307       |   |

*Elaphrus marginicollis* new species

Figs. 20, 168

*Elaphrus marginicollis* new species. Type material: Holotype male and allotype female labelled: Jack's Gulch, Roosevelt N.F., COLORADO, July 25, 1970, Coll. R. Bell; type in United States National Museum of Natural History, Washington, D.C. Additional paratypes from this and other localities mentioned below.

## Adults

**Diagnostic combination.**—Distinguished from adults of all other species of the subgenus by completely beaded lateral margin of pronotum, and by large punctures (40 to 50 microns) on pronotum and small punctures (25 microns) in elytral pits.

**Description.**—*Two color forms.* For details see color description under *E. lecontei* (p. 295) except the following. Tibiae black with metallic reflections over dorsal surface.

Antennomere 3 with few accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin moderately convex, beaded completely (Fig. 20), and not explanate before sinuation; disc with one pair of submedial impressions and without accessory setae. Metepisternum without accessory setae. Abdominal sterna of males and females with numerous accessory setae spread between ambulatory setae and lateral punctate area. Main mirror of elytron rectangular; mirrors sharply outlined, convex in three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite

Table 19. Descriptive statistics for *E. marginicollis*, based on six males and six females from Colorado, Wyoming, Washington and California.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.70–2.00	1.90	0.132	0.051	4.6
PW	1.85–2.22	2.06	0.159	0.061	5.1
EL	4.30–5.00	4.64	0.353	0.136	5.1
EW	1.60–1.95	1.73	0.166	0.064	6.4
HW	2.00–2.22	2.12	0.127	0.049	4.0
<b>B. Proportions</b>					
PL/PW	0.876–0.962	0.922	0.034	0.014	2.5
PL/EL	0.370–0.443	0.410	0.027	0.010	4.4
PL/EW	1.026–1.154	1.099	0.061	0.024	3.7
PL/HW	0.850–0.930	0.893	0.039	0.014	2.9
PW/EL	0.402–0.477	0.445	0.030	0.012	4.5
PW/EW	1.128–1.242	1.193	0.057	0.022	3.2
PW/HW	0.925–1.000	0.969	0.033	0.012	2.3
EL/EW	2.559–2.875	2.683	0.156	0.060	3.9
EL/HW	2.000–2.326	2.182	0.139	0.054	4.3
EW/HW	0.776–0.867	0.813	0.042	0.016	3.4

straight) and slightly impressed (Figs. 116, 128). Dorsal-subapical surface of hind femur with one to three short setae (Fig. 34).

**Integument sculpture.** Punctures 25 to 30 microns in diameter on head and elytra, and 40 to 50 microns in diameter on pronotum and abdomen. Punctures 20 microns apart submedially and 35 microns apart antero-laterally on pronotum, 10 microns apart in elytral pits, and 25 microns apart on elytral intervals 4, 6 and 8. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture on head, pronotum, elytral intervals, thoracic pleura and abdominal sterna (between ambulatory setae and lateral punctate area) subconvex.

**Male genitalia.** Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61). Parameres with short setae (Fig. 62b).

**Measurements and proportions.**— One sample studied. See Table 19.

**Derivation of specific epithet.**— From latin *marginalis* meaning margined and *collum* meaning neck, referring to completely beaded and margined lateral edge of pronotum.

**Distribution.**— Known from the Rocky and Siskiyou Mountains (Fig. 168).

United States. - COLORADO: Kenosha Pass (1;AMNH); Jack's Gulch, Roosevelt N.F. (8;USNM, UVCC). WYOMING: Laramie (1;USNM). WASHINGTON: Pullman (1;WSUC). CALIFORNIA: Siskiyou Co. (1;CASC).

**Collecting notes.**— At Jack's Gulch, Colorado, R.T. Bell found adults along a small spring in a sunny area on moderately firm, organic and wet soil.

**Taxonomic notes.**— I studied 12 specimens and dissected three males.

**Geographical affinities.**— The range of this species overlaps those of *E. californicus*, *E. americanus*, *E. finitimus* and *E. lecontei*.

*Elaphrus lheritieri* Antoine  
Figs. 23, 64a-b, 77a, 105, 115, 127, 168

*Elaphrus lheritieri* Antoine, 1947:26. Type locality: 35 km from Safi port between Tleta bou Guedra and Djama Sahim, Morocco; type not seen. Antoine, 1955:47. Jeanne, 1966:16.

### Adults

**Diagnostic combination.**— Distinguished from adults of all other species by immense elytral pits, and very sinuate or almost unrecognizable intervals 4, 6 and 8.

**Description.**— Only green specimens seen. For details see color under green form of *E. lecontei* (p. 295). Abdominal sterna brilliant green.

Antennomere 3 without accessory setae. Frons with clearly outlined foveola, and without accessory setae. Pronotum with lateral margin convex, obsolete and not beaded in sinuation, and clearly explanate before sinuation (Figs. 23, 77a, 105); disc with two pairs of submedial impressions, and with numerous accessory setae. Abdominal sterna of both sexes with moderate number of accessory setae between ambulatory setae. Main mirror of elytron oval; only main mirror sharply outlined and convex (Fig. 127). Elytral pits immense (intervals 4, 6 and 8 narrow and sinuated between pits), and very deeply impressed (Figs. 115, 127). Dorsal-subapical surface of hind femur with one to three short (about 60 microns) setae (Fig. 34).

**Integument sculpture.** Punctures 25 microns in diameter dorsally, and 35 microns in diameter ventrally. Punctures 10 to 20 microns apart on pronotum, 5 to 10 microns apart in elytral pits, and 10 to 15 microns apart on intervals 4, 6 and 8. First sutural pit of elytron with six or seven concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture subconvex dorsally, convex on thoracic pleura, and flat with weakly outlined meshes on abdominal sterna (surface brilliant).

**Male genitalia.** Apex of median lobe in ventral thin-edged and slightly twisted, and in lateral view axe-shaped (Figs. 64a, 64b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61). Setae of parameres long (Fig. 69c).

**Measurements and proportions.**— Based on six specimens from Abda and Safi, Morocco. PL, 1.50-1.66-1.70 mm; PW, 1.90-2.07-2.20 mm; EL, 3.80-4.12-4.30 mm; EW, 1.50-1.70-1.80 mm; HW, 1.80-1.92-2.10 mm; PL/PW, 0.756-0.800-0.821; PL/EL, 0.835-0.402-0.414; PL/EW, 0.980-0.976-1.000; PL/HW, 0.819-0.842-0.853; PW/EL, 0.477-0.503-0.542; PW/EW, 1.137-1.221-1.286; PW/HW, 1.025-1.052-1.084; EL/EW, 2.371-2.427-2.478; EL/HW, 1.025-1.052-1.084; EL/EW, 2.371-2.427-2.478; EL/HW, 2.000-2.094-2.175; EW/HW, 0.837-0.863-0.912.

**Distribution.**— Known from Morocco and northern Spain (Jeanne, 1966).

Morocco. - ABDA: (2;CJea), Safi (3;CJea, HGou), 35 km e. Safi between Tatla bou Guedra and Djama Sahim (type locality Antoine, 1955), Foucoud (Antoine, 1955). Spain. - PALENCIA: Carrion de los Condes (Antoine, 1955, and Jeanne, 1966).

**Collecting notes.**— Antoine (1947) collected adults on clay beaches of small temporary pools, "dayas", in mid-April after the winter rainy season. Adults were running during hot sunny weather between grasses on wet and dry mud. Apparently adults are not found by more permanent pools. Jeanne (1966) described the habitat as pools associated with saline soil.

**Taxonomic notes.**— This species is readily recognized from the original description.

I studied six specimens, and dissected one male.

**Geographical affinities.**— The range of this species does not overlap with those of other species.

*Elaphrus minus* new species  
Figs. 21, 77a, 168

*Elaphrus minus* new species. - Type material: Holotype male and allotype female labelled: Angwin, Cal., 5 (May) - 16 - 57, B. Cox; type in California Academy of Sciences, San Francisco.



## Adults

**Diagnostic combination.**— Distinguished by following combination: Punctures of pronotum as dense submedially as laterally (25 microns apart); pronotum and head with numerous and widespread accessory setae; two false pits present near main mirror in interval 4.

**Description.**— Two color forms. For details see under *E. lecontei* (p. 295) except the following. Intervals 4 and 6 with two false pits outlined in purple.

Antennomere 3 with few accessory setae. Frons without impression medially, and with numerous accessory setae. Pronotum with lateral margin convex, obsolete and not beaded in sinuation, and slightly explanate before sinuation (Fig. 77b); disc without submedial impressions, and with numerous and widespread accessory setae. Metepisternum with some accessory setae. Abdominal sterna of both sexes with numerous accessory setae extended between ambulatory setae and lateral punctate area. Main mirror on elytron oval; main mirror sharply outlined, others absent or suggested. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight), and slightly impressed (Figs. 116, 128). Dorsal-subapical surface of hind femur with one to three short setae (Fig. 34).

**Integument sculpture.** Punctures 25 microns in diameter on dorsal surface, and 30 to 35 microns in diameter on ventral surface. Punctures 20 to 25 microns apart on pronotum, 1 to 5 microns apart in elytral pits, and 5 to 10 microns apart on most of intervals 4, 6 and 8. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 30 to 50 punctures on each side.

Microsculpture absent or meshes weakly outlined in spots on dorsal body surface, subconvex ventrally, and flat without points on abdominal sterna.

**Male genitalia.** Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 62b). Parameres with short setae (Fig. 62b).

**Measurements and proportions.**— Based on two specimens from Anguin, California. PL, 1.6-1.7 mm; PW, 1.9-2.0 mm; EL, 4.1-4.2 mm; EW, 1.6-1.7 mm; HW, 1.9-2.0 mm; PL/PW, 0.82-0.87; PL/EL, 0.38-0.42; PL/EW, 0.95-1.09; PL/HW, 0.83-0.90; PW/EL, 0.46-0.48; PW/EW, 1.16-1.25; PW/HW, 1.01-1.03; EL/EW, 2.54-2.59; EL/HW, 2.13-2.21; EW/HW, 0.82-0.87.

**Derivation of specific epithet.**— From Latin *mimus* meaning mime or actor, referring to its apparent similarity in dorsal view with *E. finitimus* of California.

**Distribution.**— Known only from the type locality and presumed to be in the hills north of this locality (Fig. 168).

**Collecting notes.**— Found on sun exposed clay beaches of a small lake.

**Taxonomic notes.**— I studied two specimens and dissected one male.

**Geographical affinities.**— The range of this species overlaps those of *E. californicus*, *E. finitimus* and perhaps also that of *E. viridis*.

### *Elaphrus viridis* Horn

Figs. 22, 77c, 106, 114, 126, 168

*Elaphrus viridis* Horn, 1878:52. Type locality: California; type (not seen) in Museum of Comparative Zoology, Cambridge, Massachusetts. Schaupp, 1878:6. Austin, 1880:5. Bänninger, 1931:184. Lindroth, 1961:110.

*Elaphrus horni* Csiki, 1927:420. New name for *E. viridis* Horn, a junior homonym of *E. riparius* var. *viridis* Letzner, 1849:52. Lindroth (1961) rejected Csiki's name as invalid since Letzner clearly referred to a color variation of *E. riparius*. Bänninger, 1931:184. Lindroth, 1961:110.

## Adults

**Diagnostic combination.**— Distinguished from adults of other species by its magnificent and brilliant green color, and lack of outlined pits on elytra.

**Description.**— Two forms: multi-mirrors and single-mirror (along lateral margin near sinuation). In both forms: dorsal body surface bright green, except for bright copper patterns on head and pronotum and dark copper intervals 3, 5 and 7 between mirrors (same intervals bright green in single-mirror form). Ventral surface brilliant green, but abdominal sternum 6 brownish. Tibiae brown, but metallic at base and apex.

Table 20. Descriptive statistics for *E. viridis*, based on four males and six females from California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.22–1.47	1.36	0.097	0.041	4.8
PW	1.72–2.00	1.84	0.137	0.068	5.0
EL	3.55–4.05	3.74	0.276	0.116	4.9
EW	1.32–1.60	1.46	0.135	0.057	6.1
HW	1.67–1.80	1.73	0.068	0.029	2.6
B. Proportions					
PL/PW	0.689–0.775	0.741	0.042	0.018	3.8
PL/EL	0.349–0.387	0.364	0.017	0.006	3.0
PL/EW	0.879–1.038	0.930	0.072	0.030	5.2
PL/HW	0.750–0.819	0.785	0.036	0.014	3.0
PW/EL	0.475–0.507	0.491	0.017	0.008	2.2
PW/EW	1.217–1.340	1.256	0.057	0.024	3.0
PW/HW	1.015–1.127	1.060	0.052	0.022	3.3
EL/EW	2.500–2.679	2.555	0.088	0.038	2.3
EL/HW	2.058–2.250	2.158	0.091	0.038	2.8
EW/HW	0.779–0.889	0.845	0.054	0.022	4.3

Antennomere 3 with some accessory setae. Frons without medial impressions, but with numerous long accessory setae. Pronotum with lateral margin convex, unbeaded and obsolete in sinuation, and explanate before sinuation, (Figs. 22, 77c, 106); disc without submedial impressions, and with numerous long accessory setae. Metepisternum with accessory setae. Abdominal sterna of both sexes with numerous accessory setae extended to edge of sternum 5. Main mirror of elytron roughly oval; mirrors sharply outlined in three rows (Fig. 126), or only one mirror along lateral margin near sinuation. Elytral pits not impressed or outlined (Figs. 114, 126). Dorso-subapical surface of hind femur with many long setae (Fig. 35).

*Integument sculpture.* Punctures 25 microns in diameter on dorsal and ventral surface, and 15 to 25 microns in diameter on bright copper surfaces. Punctures two to five microns apart on dorsal surface, 10 to 15 microns apart on bright copper surfaces, and 25 microns apart ventrally. Number of concentric rows of punctures around setigerous punctures of elytron difficult to estimate, thus not given here. Third visible abdominal sternum with 40 to 60 punctures on each side.

Microsculpture absent dorsally, and subconvex or flat on abdominal sterna.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 62b). Setae of parameres long (Fig. 69c).

*Measurements and proportions.*— One sample studied, see Table 20.

*Distribution.*— Known from California, and rediscovered in 1967 south of Sacramento, California in the Central Valley (Fig. 168).

United States. - CALIFORNIA (9; ANSP, MCZC, CASC, INHS), Solano Co., 9.5 mi. s. Dixon (3; CASC, CNCI, UASM), Solano Co., 10 mi. s. Dixon (1; UCDC).

*Collecting notes.*— Near Dixon a few specimens were found between *Juncus* on fine clay mud. Adults were inactive in early May. The small pool was mostly dry at the start of the dry season. Kavanaugh (pers. comm.) feels that this habitat may be a refuge area at the start of the dry season, and that their true habitat would probably be flooded grassland. *E. viridis* is regarded as an endangered species, and permits must be sought to collect specimens.

**Taxonomic notes.**— The adults of this species were recognized from the original description.

I studied 13 adults, and dissected two males.

**Geographical affinities.**— The range of this species overlaps those of *E. californicus*, *E. finitimus* and perhaps also that of *E. mimus*.

*Elaphrus hypocrita* Semenov

Fig. 62a-b

*Elaphrus hypocrita* Semenov, 1926:39. Type area: Russian Turkestan; type not seen.

*Elaphrus smaragdiceps*; Bänninger, 1919:148 (*nec* Semenov, 1889). Semenov, 1926:39.

### Adults

**Diagnostic combination.**— Among Palaearctic species, adults are easily recognized by restricted distribution of accessory setae on abdominal sterna (not extended to lateral edge), by short setae on parameres, and by brilliant abdominal sterna (excluding *E. comatus*). In relation to all species, adults of this species are best characterized by character combination in key.

**Description.**— Two color forms. For details see under *E. lecontei* (p. 295) except the following. Intervals 4 and 6 without false pits outlined in purple.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, unbeaded and suggested in situation, and not explanate in front of situation (Figs. 25, 77d); disc with one pair of impressions submedially and without accessory setae. Metepisternum without accessory setae. Abdominal sterna in males and females with scattered accessory setae between ambulatory setae. Main mirror of elytron rectangular; main mirror sharply outlined, others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight), and slightly impressed (Fig. 116). Dorso-subapical surface of hind femur with one or two short (40 to 50 microns) setae (Fig. 34).

**Integument sculpture.** Punctures 20 to 25 microns in diameter dorsally, and 30 to 35 microns in diameter ventrally. Punctures 15 to 25 microns apart medially and 30 to 40 microns apart antero-laterally on pronotum, 5 to 10 microns apart in elytral pits, 10 to 20 microns apart on elytral intervals 4, 6 and 8, and 30 microns apart on proepisternum. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture convex or subconvex on most of dorsal body surface and thoracic pleura, and flat on abdominal sterna especially between ambulatory setae and lateral margin, surface brilliant.

**Male genitalia.** Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 62a, 62b); base of lobe along ventral angular bend narrowly sclerotized with ventral membrane visible in lateral view (Fig. 61). Setae of parameres short (Fig. 62b).

**Measurements and proportions.**— Based on six specimens from Wernyi (old Turkestan). PL, 1.5-1.67-1.7 mm; PW, 1.6-1.80-1.9 mm; EL, 3.9-4.16-4.3 mm; EW, 1.5-1.59-1.6 mm; HW, 1.7-1.91-2.0 mm; PL/PW, 0.917-0.924-0.932; PL/EL, 0.385-0.400-0.407; PL/EW, 1.000-1.049-1.079; PL/HW, 0.835-0.873-0.893; PW/EL, 0.417-0.433-0.442; PW/EW, 1.083-1.136-1.161; PW/HW, 0.911-0.945-0.974; EL/EW, 2.585-2.622-2.667; EL/HW, 2.063-2.183-2.234; EW/HW, 0.785-0.832-0.857.

**Distribution.**— Known from the north shore of the Black Sea to western China (Semenov, 1926).

**Taxonomic notes.**— I studied six adults and dissected two males.

**Geographical affinities.**— The range of this species overlaps that of *E. riparius*.

*Elaphrus ruscarius* Say

Figs. 60a-b, 109, 168

*Elaphrus ruscarius* Say, 1834:417. Type locality: Pennsylvania subsequently designated by Lindroth (1961); Lindroth and Freitag (1969) designated a male from Columbia, Penn. as neotype; the neotype is in the LeConte Collection in the Museum of Comparative Zoology, Cambridge, Massachusetts. Say, 1823:496. 1834:529. LeConte,

Table 21. Descriptive statistics for *E. ruscarius*, based on ten males and nine females from Vermont.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.54	0.094	0.029	4.1
PW	1.50–1.87	1.68	0.149	0.046	5.9
EL	3.40–4.15	3.82	0.294	0.090	5.1
EW	1.40–1.65	1.53	0.115	0.035	5.0
HW	1.70–2.00	1.86	0.110	0.034	3.9
B. Proportions					
PL/PW	0.836–1.048	0.919	0.069	0.022	5.0
PL/EL	0.375–0.441	0.402	0.024	0.008	4.0
PL/EW	0.955–1.053	1.008	0.040	0.012	2.7
PL/HW	0.773–0.880	0.827	0.039	0.012	3.1
PW/EL	0.414–0.467	0.438	0.024	0.004	3.6
PW/EW	1.000–1.197	1.099	0.066	0.020	4.0
PW/HW	0.840–0.945	0.901	0.048	0.014	3.5
EL/EW	2.386–2.667	2.506	0.102	0.032	2.7
EL/HW	1.947–2.192	2.057	0.109	0.034	3.5
EW/HW	0.760–0.868	0.821	0.043	0.014	3.5

1853:401. Crotch, 1873:4. Mäklin, 1877:17. Schaupp, 1878:6. Blatchley, 1910:48 (*ex parte*). Bänninger, 1919:148. Hatch, 1953:63. Lindroth, 1961:119. Lindroth and Freitag, 1969:332.

*Elaphrus americanus*; LeConte, 1853:402. Mäklin, 1877:17. *nec* Dejean, 1831.

*Elaphrus texanus* Casey, 1924:17. Type locality: Galveston, Texas; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:119.

Adults

*Diagnostic combination*.— Distinguished from adults of other species by apparently large proepisternal punctures (60 microns). In reality punctures 30 to 40 microns, but appearing larger since areas around them are depressed.

*Description*.— Two color forms. For details see under *E. lecontei* (p. 295) except following. Ventral punctures blue-green; smooth and microsculptured surface of thoracic pleura dark copper (almost black on propleuron), and green elsewhere.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obsolete and not beaded in situation, and not explanate before sinuation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and without accessory setae. Abdominal sterna of both sexes with numerous accessory setae between ambulatory setae and lateral punctate area. Main mirror of elytron rectangular; one to three subsutural mirrors sharply outlined, others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and moderately impressed. Dorsal-subapical surface of hind femur with one or two short (40 to 60 microns) setae (Fig. 34).

*Integument sculpture*. Punctures 25 to 30 microns in diameter on most of head, pronotum and elytra, and 30 to 40 microns in diameter on elytral pits, abdominal sterna and thoracic pleura. Punctures 20 microns apart on elytral intervals 4, 6 and 8, submedially on pronotum and on head, 5 to 15 microns apart in elytral pits, 35 microns apart on thoracic pleura, on abdominal sterna, and antero-laterally on pronotum. First sutural pit of elytron with three to four concentric rows of punctures. Third visible abdominal sternum with 30 to 40 punctures on each side.

Microsculpture convex or subconvex over most of dorsal body surface and thoracic pleura, and flat and without points on abdominal sterna between ambulatory setae and lateral punctate area.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 60a, 60b); base of lobe along ventral angular bend widely sclerotized, and ventral membrane not visible in lateral view. Setae of parameres long (Fig. 69c).

*Measurements and proportions.*— Five samples studied, and data for one presented in Table 21.

*Variation.*— Between northern and southern samples no obvious differences were observed. Copper coloured individuals are known to me only from regions with red soils. This color form is probably cryptic on these soils.

### All Instar Larvae

*Diagnostic combination.*— Recognized from larvae of other species by combination of characters in key.

### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much larger than that on terga. Seta AIM on terga abruptly short, at least on tergum 8. Antero-dorsal seta of abdominal epipleura 1 and 8 very small, and markedly larger on epipleura 2 to 7.

### Second and Third Instar Larvae

*Description.*— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— Restricted to eastern North America, from the Atlantic coast to the prairies, and from northern Minnesota and southern Maine in the north, to southern Georgia, Louisiana and eastern Texas in the south (Fig. 168).

*Collecting notes.*— Found on many types of wet beaches (clay, sand, silt and organic) in swamps, along small rivers and ditches. The substrate is usually free of vegetation and sun-exposed.

*Taxonomic notes.*— Casey's holotype (*E. texanus*) represents a typical adult of this species.

I studied more than 4000 adults, and dissected six males. I examined two first, one second and on third instar larvae from northern Arkansas.

*Geographical affinities.*— The range of this species overlaps those of *E. californicus*, *E. americanus* (marginally) and *E. lecontei* (marginally).

### *Elaphrus lecontei* Crotch.

Figs. 13, 24, 65a-b, 75, 81, 91a-b, 130, 169

*Elaphrus lecontei* Crotch, 1876:246. Type locality: Longs Peak, Colorado; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. Crotch, 1873:6. Schaupp, 1878:6. La Rivers, 1946:138. Hatch, 1953:63. Lindroth, 1961:114.

*Elaphrus intermedius* LeConte, 1848:448 (*nec* Kirby, 1837). Crotch, 1873:6. 1876:246. Schaupp, 1878:6. Lindroth, 1961:114.

*Elaphrus devinctus* Casey, 1920:139. Type locality: Wray, Colorado; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington D.C. Lindroth, 1961:114.

*Elaphrus spissicornis* Casey, 1924:18. Type locality: Parowan, Utah; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:114.

Table 22. Descriptive statistics for *E. lecontei*, based on ten males and nine females from Manitoba.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.62–1.95	1.79	0.133	0.041	4.9
PW	2.00–2.32	2.16	0.144	0.044	4.4
EL	4.10–4.85	4.45	0.349	0.107	5.2
EW	1.57–1.90	1.75	0.138	0.042	5.3
HW	2.00–2.27	2.11	0.121	0.037	3.8
B. Proportions					
PL/PW	0.772–0.878	0.831	0.040	0.012	3.2
PL/EL	0.374–0.431	0.399	0.021	0.006	3.5
PL/EW	0.956–1.108	1.026	0.066	0.020	4.3
PL/HW	0.802–0.889	0.852	0.037	0.012	2.9
PW/EL	0.454–0.506	0.481	0.019	0.006	2.7
PW/EW	1.178–1.299	1.234	0.057	0.018	3.1
PW/HW	0.976–1.095	1.026	0.046	0.014	3.0
EL/EW	2.429–2.716	2.568	0.102	0.032	2.6
EL/HW	2.000–2.259	2.136	0.111	0.034	3.5
EW/HW	0.782–0.881	0.832	0.043	0.014	3.5

## Adults

**Diagnostic combination.**— Distinguished from adults of other species by wider pronotum with sharply delineated anterior transverse stria toward anterior angle (Fig. 24), by dense pubescence on antennomere 3, and by six to ten rows of puncture in first sutural pit of elytron.

**Description.**— Two color forms. Green form: microsculptured and smooth surfaces dark copper on most of elytra, on portions of pronotum and head, bright copper on portions of pronotum and head, and purple near center of elytral pits; punctures green but purple near center of elytral pits. Ventral punctures green; smooth and microsculptured surfaces dark copper on pleura and green on abdominal sterna. Copper form: as above but punctures copper dorsally. In both forms: interval 4 with purple false pit near main mirror in many specimens; tibia red-brown and metallic at base and apex.

Antennomere 3 setose in apical 0.5, especially along posterior side (Fig. 13). Frons without medial impression and accessory setae. Pronotum with lateral margin convex, obliterated and not beaded in situation, and not explanate before situation (Figs. 24, 77d); disc with one or two pairs of submedial impressions, without accessory setae, with sharply defined antero-transverse stria toward anterior angle, and generally with mirrors near main submedial impression (Fig. 24). Abdominal sterna with sparse setae between ambulatory setae; setae more numerous in males than in females. Main mirror of elytron rectangular; mirrors sharply outlined on intervals 3, 3 and 5, or 3, 5 and 7; mirrors absent or developed in elytral pits. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly to deeply impressed (Fig. 130). Dorso-subapical surface of hind femur with one to three short (40 to 60 microns) setae (Fig. 34).

**Integument sculpture.** Punctures 20 to 25 microns in diameter on dorsal body surface, 25 to 30 microns in diameter on abdominal sterna, and 30 to 35 microns in diameter on thoracic pleura. Punctures 2 to 5 microns apart in elytral pits, 2 to 15 microns apart on elytral intervals, submedially on pronotum, and on head, 20 to 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit with six to ten concentric rows of punctures. Abdominal sternum 3 with 70 to 100 punctures on each side.

Microsculpture of dorsal body surface generally absent or meshes weakly outlined, but in spots subconvex or convex on thoracic pleura, and flat or subconvex on abdominal sterna between ambulatory setae and lateral punctate portion.

**Male genitalia.** Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view wide and long (Figs. 65a, 65b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres long (Fig. 69c).

Table 23. Descriptive statistics for *E. lecontei*, based on ten males and ten females from Lower Klamath Lake, Oregon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.67–1.95	1.85	0.116	0.035	4.2
PW	2.00–2.40	2.21	0.148	0.044	4.5
EL	4.35–5.40	4.84	0.412	0.123	5.7
EW	1.67–2.02	1.83	0.150	0.045	5.4
HW	2.00–2.27	2.15	0.120	0.036	3.7
B. Proportions					
PL/PW	0.774–0.905	0.836	0.046	0.014	3.7
PL/EL	0.349–0.442	0.382	0.028	0.008	5.0
PL/EW	0.905–1.087	1.008	0.072	0.022	4.8
PL/HW	0.807–0.905	0.859	0.040	0.012	3.1
PW/EL	0.432–0.484	0.457	0.021	0.006	3.1
PW/EW	1.122–1.294	1.206	0.063	0.018	3.5
PW/HW	1.000–1.060	1.027	0.030	0.008	1.9
EL/EW	2.553–2.750	2.640	0.079	0.024	2.0
EL/HW	2.140–2.374	2.249	0.105	0.032	3.1
EW/HW	0.800–0.892	0.852	0.037	0.012	2.9

*Measurements and proportions.*— Fifteen samples studied, and data for three presented in Tables 22 to 24.

*Variation.*— Specimens from the San Luis Valley in southern Colorado are strikingly different from any other samples. In this area adults are characterized as follows: all elytral mirrors convex and sharply outlined; mirrors developed in elytral pits and near submedial impression of pronotum; punctures larger dorsally as shown by fewer rows of punctures in pit anterior to main mirror; elytra more convex (similar to adults of *E. californicus*). Remaining samples show more subtle differences and are discussed in a coming study on variation among populations.

#### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by very small seta VEM-P on parietale, and by subequal seta PII=P on nota and terga.

#### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.3 to 0.5 as long as antennomere 1. Seta VEM-P of parietale very small. Seta PII-P of nota very small and subequal to that on terga. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleura markedly smaller than on segments 3 to 5.

Table 24. Descriptive statistics for *E. lecontei*, based on ten males and ten females from Lone Pine, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.85–2.15	2.03	0.104	0.031	3.4
PW	2.30–2.70	2.52	0.129	0.038	3.4
EL	4.70–5.50	5.12	0.298	0.089	3.9
EW	1.82–2.15	2.02	0.112	0.033	3.7
HW	2.22–2.55	2.39	0.103	0.031	2.9
B. Proportions					
PL/PW	0.769–0.835	0.807	0.021	0.006	1.7
PL/EL	0.377–0.426	0.398	0.019	0.006	3.3
PL/EW	0.965–1.025	1.009	0.046	0.014	3.1
PL/HW	0.814–0.887	0.851	0.028	0.008	2.2
PW/EL	0.468–0.510	0.493	0.021	0.006	2.8
PW/EW	1.198–1.299	1.250	0.045	0.014	2.4
PW/HW	1.031–1.103	1.055	0.027	0.016	1.7
EL/EW	2.447–2.625	2.537	0.075	0.022	2.0
EL/HW	2.040–2.245	2.142	0.079	0.026	2.8
EW/HW	0.808–0.878	0.844	0.028	0.008	2.3

### Second Instar Larvae

*Description.*— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

### Third Instar Larvae

*Description.*— Head paler at base than behind eyes, and pronotum pale in lateral 0.3.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— Known from grasslands of western North America where there are alkaline marshes or creeks, but isolated near Great Slave Lake and along James Bay(2;CSWC, CNCI) (Fig. 169).

*Collecting notes.*— Adults are found on sun-exposed alkaline beaches of lakes, marshes and creeks. In most of the range, adults occur only near slightly alkaline waters, but in California, Utah and Great Slave Lake, Northwest Territories, they are also found on deeply crusted alkaline beaches. Beaches are free of vegetation, and are in relatively sheltered areas (especially near lakes). Adults run even on water-saturated soil near water edge, and are found under small stones or in crevices when inactive. The soil of upper beaches, in some of the localities studied, is red, thus copper individuals, in spring time, would be cryptically colored.

*Taxonomic notes.*— The holotype of *E. divinctus* Casey matches specimens of *E. lecontei* east of the Rockies, while that of *E. spissicornis* Casey matches those west of the Rockies. The first mention of the specific epithet *lecontei* by Crotch (1873:6) was not valid as there was no description. Crotch (1873) very ambiguously referred to a specimen identified and keyed as *E. intermedius* by LeConte (1848:448).



Table 25. Descriptive statistics for *E. californicus*, based on ten males and ten females from Maryland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.50–1.75	1.59	0.108	0.032	4.5
PW	1.55–1.85	1.66	0.131	0.039	5.3
EL	3.25–3.87	3.55	0.252	0.075	4.7
EW	1.35–1.60	1.48	0.108	0.032	4.8
HW	1.75–2.00	1.90	0.108	0.032	3.8
B. Proportions					
PL/PW	0.863–1.015	0.961	0.055	0.016	3.8
PL/EL	0.426–0.465	0.450	0.016	0.004	2.4
PL/EW	0.984–1.155	1.077	0.057	0.016	3.5
PL/HW	0.772–0.875	0.839	0.042	0.012	3.3
PW/EL	0.441–0.493	0.469	0.021	0.006	3.0
PW/EW	1.083–1.185	1.121	0.043	0.012	2.6
PW/HW	0.838–0.925	0.874	0.039	0.012	3.0
EL/EW	2.295–2.552	2.393	0.105	0.032	2.9
EL/HW	1.757–1.959	1.865	0.084	0.024	3.0
EW/HW	0.753–0.810	0.780	0.024	0.008	2.1

I studied more than 1000 adults, and dissected ten males. I examined six first instar, five second instar and three third instar larvae from Miquelon Lakes Provincial Park, Alberta.

*Geographical affinities.*— The range of this species overlaps those of *E. californicus*, *E. finitimus*, *E. americanus*. In its extreme eastern limit its range overlaps that of *E. ruscarius*. The range of *E. marginicollis*, a high altitude species, is probably parapatric with that of *E. lecontei*.

*Elaphrus californicus* Mannerheim

Figs. 35, 77d, 140, 154, 155, 172

*Elaphrus californicus* Mannerheim, 1843:190. Type locality: California; lectotype, designated by Lindroth, in Zoological Museum, University of Helsinki, Finland. LeConte, 1853:402. Crotch, 1876:246. Schaupp, 1878:6. Lindroth, 1961:118.

*Elaphrus similis* LeConte, 1848:449. Type locality: Longs Peak, Colorado; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:402. Schaupp, 1878:6. Lindroth, 1961:118.

*Elaphrus intermedius*; Walker, 1866:309 (*nec* Kirby, 1837).

*Elaphrus riparius*; Crotch, 1873:4 (*ex parte*). Schaupp, 1878:6 (*ex parte*). Taylor, 1886:35 (*ex parte*). Harrington, 1889:139 (*ex parte*). Venables, 1913:26 (*ex parte*). Hippiusley, 1922:63 (*ex parte*). La Rivers, 1946:138 (*ex parte*). Clark 1948:25 (*ex parte*). Hatch, 1953:63 (*ex parte*). *nec* Linnaeus, 1758.

*Elaphrus ruscarius*; Blatchley, 1910:48 (*ex parte*) (*nec* Say, 1834).

*Elaphrus hesperius* Casey, 1920:138. Type locality: Humboldt Co., California; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:118.

Table 26. Descriptive statistics for *E. californicus*, based on ten males and ten females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.55	0.093	0.028	4.0
PW	1.52–1.77	1.63	0.114	0.035	4.8
EL	3.50–4.00	3.69	0.219	0.066	4.0
EW	1.40–1.60	1.49	0.091	0.027	4.1
HW	1.70–1.97	1.84	0.109	0.033	4.0
B. Proportions					
PL/PW	0.900–1.016	0.953	0.048	0.014	3.6
PL/EL	0.399–0.438	0.422	0.015	0.004	2.4
PL/EW	0.966–1.103	1.044	0.046	0.014	3.0
PL/HW	0.817–0.878	0.846	0.025	0.008	2.0
PW/EL	0.420–0.467	0.443	0.019	0.006	2.9
PW/EW	1.066–1.138	1.096	0.033	0.010	2.0
PW/HW	0.840–0.945	0.888	0.045	0.014	3.4
EL/EW	2.323–2.554	2.476	0.089	0.026	2.4
EL/HW	1.896–2.164	2.006	0.084	0.024	2.8
EW/HW	0.753–0.868	0.811	0.039	0.012	3.2

## Adults

**Diagnostic combination.**— Distinguished from adults of other species by following character combination: dorso-apical setae on hind femur long; proepisternal punctures dense (10 to 20 microns apart); accessory setae on abdominal sterna sparse.

**Description.**— In most populations one color form: gray-green or almost black, but in other populations, with bicolored individuals. Gray-green form: microsculptured and smooth surfaces on dorsal surface brass to black, copper in spots on pronotum and head, and purple near center of pits; punctures blue-green but purple near center of pits. Ventral surface with green punctures; microsculptured and smooth surfaces red purple on proepisternum, brass on other pleura, and green on sterna. Bicolored form: head, pronotum and extreme base of elytra as for gray-green form; rest of elytra with microsculptured and smooth surfaces black or copper; punctures almost black or dark copper (elytra at low magnification appear black), or copper (elytra at low magnification appear red-purple); pits better outlined with large copper punctures in outer 0.3. Black form (southern Oregon and adjacent California): microsculptured and smooth areas brilliant black dorsally; punctures dark blue-green, and pits better outlined with large green punctures in outer 0.3 (dorsal surface, at low magnification, appear much darker as mirrors are mostly fused). In all forms, interval 4 of some specimens with purple false pit near main mirror; tibiae red-brown, but metallic at base and apex.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin little convex, obliterated and not beaded in situation, and not explanate before situation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and without accessory setae. Abdominal sterna with few scattered setae; setae more numerous in males than in females. Main mirror of elytron rectangular; main mirror well outlined, others suggested or absent, but in black form most mirrors well outlined and fused with others. Elytral pits moderately wide (interval 4,6 and 8 quite straight) and generally quite impressed. Dorso-subapical surface of hind femur with five to ten long (80 to 150 microns) setae (Fig. 35).

**Integument sculpture.** Punctures 20 to 25 microns in diameter dorsally (generally 15 to 20 microns in prairie region), 30 microns in diameter along outer margin of pits, and 35 to 40 microns in diameter on abdominal sterna and thoracic pleura. Punctures 2 to 5 microns apart in elytral pits, 10 to 15 microns apart on elytral intervals (but 10 to 30 microns apart in black form), 5 to 10 microns apart medially and 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit of elytron with four to six concentric rows of punctures. Third visible

Table 27. Descriptive statistics for *E. californicus*, based on ten males and ten females from Seattle, Washington.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.87	1.73	0.114	0.034	4.4
PW	1.67–1.92	1.88	0.100	0.030	3.8
EL	3.50–4.25	3.93	0.283	0.084	4.8
EW	1.40–1.62	1.56	0.100	0.030	4.3
HW	1.75–2.07	1.92	0.108	0.035	4.1
B. Proportions					
PL/PW	0.905–1.014	0.959	0.043	0.012	3.0
PL/EL	0.404–0.463	0.441	0.024	0.008	3.6
PL/EW	1.047–1.175	1.110	0.051	0.016	3.1
PL/HW	0.873–0.948	0.902	0.033	0.010	2.4
PW/EL	0.432–0.487	0.461	0.024	0.008	3.5
PW/EW	1.092–1.224	1.158	0.050	0.014	2.8
PW/HW	0.875–0.987	0.941	0.042	0.012	3.0
EL/EW	2.413–2.596	2.516	0.085	0.026	2.3
EL/HW	1.900–2.184	2.046	0.114	0.034	3.7
EW/HW	0.771–0.855	0.813	0.037	0.012	3.1

abdominal sternum with 150 to 200 punctures on each side. Microsculpture generally convex dorsally (generally absent in black form) and ventrally on thoracic pleura, and subconvex on abdominal sterna.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 61a and 61b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres short (Fig. 62b).

*Measurements and proportions.*— Thirty-seven samples studied, and data for four presented in Tables 25 to 28.

*Variation.*— A study of this polytypic species is in progress. The following is a summary of more obvious variables. In central Pennsylvania southward, adults are generally golden and only the main mirror is outlined. North of this region to central Minnesota all adults are green. West of this region to central British Columbia adults are either gray-green or bicolored. The bicolored form gradually disappears from British Columbia to northernmost California and Utah. Along the Pacific coast, adults are darker. East of the Cascades, adults become progressively darker southward, and in southern Oregon and adjacent California they are brilliant and almost black. Along the Colorado Plateau, south to northern New Mexico, adults resemble those from British Columbia. From the black form of northern California adults become progressively greener and more densely punctate southward. This last type extends across Nevada to southwestern Wyoming. In central California there is a large form. In the Siskiyou and Trinity Mountain region only, a portion of individuals of this form are bicolored (red-purple elytra).

Table 28. Descriptive statistics for *E. californicus*, based on ten males and ten females from Susanville, California and Quincy, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.65–1.90	1.76	0.114	0.034	4.3
PW	1.75–2.02	1.89	0.136	0.041	4.8
EL	3.85–4.25	4.02	0.200	0.060	3.2
EW	1.52–1.75	1.61	0.090	0.027	3.7
HW	1.87–2.10	1.98	0.100	0.030	3.4
B. Proportions					
PL/PW	0.887–1.000	0.932	0.042	0.012	3.0
PL/EL	0.411–0.463	0.437	0.018	0.006	2.7
PL/EW	1.031–1.134	1.089	0.043	0.014	2.7
PL/HW	0.855–0.938	0.889	0.036	0.010	2.7
PW/EL	0.443–0.488	0.469	0.021	0.006	3.0
PW/EW	1.094–1.231	1.169	0.058	0.018	3.3
PW/HW	0.875–1.012	0.954	0.042	0.012	2.9
EL/EW	2.382–2.576	2.490	0.072	0.022	1.9
EL/HW	1.949–2.125	2.032	0.073	0.022	2.4
EW/HW	0.775–0.875	0.816	0.036	0.010	2.9

### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by short epicranial suture (0.2 to 0.3 length of antennomere 1), and by very small anterior seta of abdominal epipleura 1 to 8.

### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.2 to 0.3 as long as antennomere 1. Seta VEM-p of parietale small. Seta PII-P of nota much longer than that on terga. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleura 1 to 8 subequal and very small.

### Second and Third Instar Larvae

*Description.*— Head brown behind eyes, nota and terga dark brown, and urogomphus brown.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— Transcontinental in North America. It is known almost from the tree line south to extreme southern California, Northern New Mexico, Texas, Louisiana and Florida. Adults were not collected along the Pacific coast north of Washington state (Fig. 172).

*Collecting notes.*— In most regions, adults are exclusively associated with clay beaches, free of vegetation along creeks, dugouts and ditches. In California adults are found on sandy, silty and clayish beaches. Excluding modified habitats, this species is normally found along small rivers (except for specimens from Pennsylvania southward) where wave and wind action is

Table 29. Descriptive statistics for *E. finitimus*, based on four males and three females from White Mountains, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.50–1.85	1.65	0.173	0.087	7.0
PW	1.60–2.00	1.81	0.182	0.092	6.7
EL	4.00–4.50	4.27	0.273	0.138	4.3
EW	1.60–1.85	1.72	0.156	0.051	6.0
HW	1.80–2.00	1.89	0.123	0.073	4.3
B. Proportions <sup>1</sup>					
PL/PW		0.910	0.031	0.015	2.3
PL/EL		0.386	0.029	0.014	5.0
PL/EW		0.978	0.041	0.028	2.8
PL/HW		0.884	0.079	0.047	6.0
PW/EL		0.425	0.026	0.013	4.1
PW/EW		1.080	0.024	0.016	1.5
PW/HW		0.979	0.063	0.038	4.3
EL/EW		2.520	0.115	0.077	3.0
EL/HW		2.300	0.116	0.069	3.4
EW/HW		0.902	0.059	0.039	4.4

<sup>1</sup>Values for "Range" not available.

minimal. Beaches are sun-exposed and almost horizontal. Adults run mostly on the moist portions, but avoid the saturated portions.

*Taxonomic notes.*— The holotype of *E. hesperius* matches adults of the California population, and that of *E. similis* those of Rocky mountain populations.

I have studied about 3000 adults, and dissected more than 100 males. I examined four first instar, eight second instar and six third instar larvae from George Lake, Alberta.

*Geographical affinities.*— The range of this species overlaps those of all North American species of the subgenus, except that of *E. parviceps*. I have found specimens in a few localities with adults of *E. finitimus*, *E. americanus* and *E. lecontei*, but, in these situations, adults of these other species were rare. However, I found adults of *E. ruscarius* and of *E. californicus* in equal numbers on clay beaches.

*Elaphrus finitimus* Casey

Figs. 66a-b, 170

*Elaphrus finitimus* Casey, 1920:137. Type locality: California; type (seen by me) in United States National Museum of Natural History, Washington, D.C.

*Elaphrus ruscarius foveatus* Pierce, 1948a:54. Type locality: McKittrick asphalt field, site 4 depth four feet, Los Angeles, California; type (seen by me) in Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

*Elaphrus riparius*; La Rivers, 1946:138 (*ex parte*) (*nec* Linnaeus, 1758).

*Elaphrus americanus*; Lindroth, 1961:115 (*ex parte*) (*nec* Dejean, 1831).

Table 30. Descriptive statistics for *E. finitimus*, based on ten males and seven females from Martin Springs, Lassen Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.85	1.68	0.115	0.037	4.6
PW	1.70–2.10	1.88	0.163	0.053	5.8
EL	3.90–4.65	4.32	0.291	0.094	4.5
EW	1.45–1.70	1.60	0.156	0.050	6.5
HW	1.75–1.95	1.84	0.104	0.033	3.8
B. Proportions <sup>1</sup>					
PL/PW		0.897	0.036	0.012	2.7
PL/EL		0.390	0.018	0.006	3.1
PL/EW		1.050	0.083	0.027	5.3
PL/HW		0.911	0.031	0.010	2.3
PW/EL		0.435	0.020	0.006	3.1
PW/EW		1.170	0.109	0.035	6.2
PW/HW		1.010	0.049	0.015	3.2
EL/EW		2.700	0.202	0.065	5.0
EL/HW		2.340	0.105	0.034	3.0
EW/HW		0.868	0.071	0.023	5.4

<sup>1</sup>Values for "Range" not available.

## Adults

**Diagnostic combination.**— Distinguished from adults of all species (excluding *E. americanus*) by character combination in key. From *E. americanus* separated as follows: in males of *E. finitimus*, median lobe long (4.6 to 5.3 mm), and its apex in ventral view thin-edged.

**Description.**— Two color forms. Green form: microsculptured and smooth surfaces dark copper or black (specimens from Sierra Nevada, White Mountains of California, and northeastern California) dorsally, copper in spots on head and pronotum, and purple near center of pits; punctures green or blue-green (specimens from northeastern California), and purple near center of pits. Ventral coloration as for *E. lecontei*. Copper form (known from Intermontane Region) colored as green form, but punctures generally copper. In both forms: interval 4 of many specimens with purple false pit near main mirror; tibiae red-brown, but metallic at base and apex.

Antennomere 3 with or without few accessory setae. Frons without medial impression, and, in many specimens from northeastern California and adjacent Oregon, with numerous accessory setae. Pronotum with lateral margin slightly convex (Fig. 25), obliterated and not beaded in situation, and not explanate before situation (Fig. 77d); disc with one or two pairs of submedial impressions, and with accessory setae in some specimens in Intermontane Region. Abdominal sterna with numerous accessory setae between ambulatory setae and lateral punctate area; setae more numerous in males than in most females. Main mirror of elytron rectangular; mirrors in first row generally well outlined, but specimens from Colorado Plateau with two or three rows of sharply delineated mirrors. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly to deeply impressed. Dorso-subapical surface of hind femur with one or two short (40 microns) setae (Fig. 34).

**Integument sculpture.** Punctures 20 to 25 microns in diameter on head, pronotum and elytra, 30 microns in diameter along outer half of elytral pits and abdominal sterna, and 35 to 40 microns in diameter on thoracic pleura. Punctures 2 to 10 microns apart in elytral pits, portions of pronotum and head, 10 to 20 microns apart on most of elytral intervals 4, 6 and 8 and on proepisternum, and 30 to 40 microns apart antero-laterally on pronotum. First sutural pit of elytron with three to six concentric rows of punctures. Abdominal sternum 3 with 150 to 200 punctures on each side.

Table 31. Descriptive statistics for *E. finitimus*, based on eleven males and nine females from Williams, Arizona.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.57–1.85	1.66	0.099	0.029	4.0
PW	1.67–2.05	1.81	0.134	0.040	4.9
EL	3.90–4.67	4.17	0.258	0.077	4.1
EW	1.45–1.85	1.58	0.135	0.040	5.7
HW	1.75–2.02	1.85	0.099	0.029	3.6
<b>B. Proportions<sup>1</sup></b>					
PL/PW		0.919	0.043	0.013	3.1
PL/EL		0.399	0.018	0.005	3.0
PL/EW		1.060	0.068	0.020	4.3
PL/HW		0.896	0.027	0.008	2.0
PW/EL		0.434	0.014	0.004	2.1
PW/EW		1.150	0.049	0.015	2.8
PW/HW		0.976	0.039	0.012	2.7
EL/EW		2.650	0.104	0.031	2.6
EL/HW		2.250	0.096	0.029	2.8
EW/HW		0.850	0.048	0.014	3.8

<sup>1</sup>Values for "Range" not available.

Microsculpture outlined over part of or absent from intervals 4, 6 and 8, convex on thoracic pleura, and flat or subconvex (rarely with some pointed microsculpture) on abdominal sterna.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view; lobe long: distance from angular bend to apex 4.6 to 5.3 mm. Setae of parameres long (Fig. 69c).

*Measurements and proportions.*— Twenty samples studied, and data for four presented in Tables 29 to 32.

*Variation.*— The following is a brief characterization of the seven populations recognized (Goulet and Baum, 1982). The Colorado Plateau form: large; two to three rows of mirrors on elytra; 7% of specimens copper dorsally; accessory setae (seen in few individuals) on pronotum only. The western Great Basin form: dark; accessory setae (in most specimens) on head and pronotum. The White Mountains of California form: almost black; adults of moderate size; head and pronotum without accessory setae. The central California form: punctures dense, all adults green, head and pronotum without accessory setae. The southern California form: similar to that from central California but punctures, especially in elytral pits, much larger. In southern Sierra Nevada a dark and deeply pitted form with large punctures in pits is found. The sample from northwestern Arizona resembles those of central California, but differs from them in having 30% of specimens copper.

### Third Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by character combination in key.

Table 32. Descriptive statistics for *E. finitimus*, based on seven males and twelve females from Sonoma Co., California and Marin Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.60–1.75	1.67	0.069	0.021	2.7
PW	1.70–1.90	1.80	0.100	0.030	3.7
EL	3.75–4.35	4.11	0.237	0.072	3.8
EW	1.50–1.90	1.60	0.096	0.029	4.0
HW	1.80–1.90	1.85	0.057	0.017	2.1
B. Proportions <sup>1</sup>					
PL/PW		0.929	0.042	0.013	3.1
PL/EL		0.405	0.018	0.006	3.0
PL/EW		1.040	0.057	0.017	3.7
PL/HW		0.900	0.030	0.009	2.2
PW/EL		0.438	0.024	0.007	3.6
PW/EW		1.120	0.053	0.016	3.2
PW/HW		0.970	0.044	0.013	3.0
EL/EW		2.570	0.138	0.042	3.6
EL/HW		2.220	0.090	0.028	2.7
EW/HW		0.864	0.041	0.013	3.2

<sup>1</sup>Values for "Range" not available.

*Description.*— Very similar to same instar of *E. americanus* except microsculpture on tergal bands more restricted: pointed microsculpture on about 50% of posterior band laterally, and absent from anterior band.

#### Geographical Distribution and Affinities, and Notes

*Distribution.*— A western North American species associated with forested regions, from southern Oregon to western Montana in the north, to southernmost California, northern Arizona and southern Colorado in the south (Fig. 170).

*Collecting notes.*— I collected large series of this species around Petaluma, California on wet clay beaches. Beaches were sun-exposed, protected from winds and strong wave action, and free of vegetation. I have no data from other areas of its range, though G.E. Ball (pers. comm.) collected one adult from southern Idaho in a similar habitat.

*Taxonomic notes.*— The fossil specimen of *E. ruscarius foveatus* is represented by one complete elytron. The elytron best matches that of *E. americanus* or *E. finitimus*. Microsculpture, puncture density on elytral intervals 4, 6 and 8 and shape of pit behind main mirror suggest the above association. I am not able to ascertain which of the two species this elytron represents but it matches perfectly extant western Californian specimens of *E. finitimus*.

I have studied about 1000 adults and dissected more than 100 males. I examined one third instar larva.

*Geographical affinities.*— The range of *E. finitimus* overlaps those of *E. marginicollis*, *E. viridis*, *E. mimus*, *E. lecontei* and *E. californicus*. In the same habitat few specimens of *E.*



*californicus* may be found with those of *E. finitimus*.

*Elaphrus americanus* Dejean

**Adults**

*Diagnostic combination*.— Distinguished from adults of all species (except those of *E. finitimus*) by character combination in key. Distinguished from adults of *E. finitimus* as follows. In males of *E. americanus*, median lobe short (3.5 to 4.7 mm), and its apex in ventral view thick-edged (Figs. 67a, 68a, 69a).

*Variation*.— Goulet and Baum (1981) distinguished two subspecies. One is restricted to boreal regions, from the arctic treeline south to central British Columbia, and east to Newfoundland. The other extends along the Pacific coast from British Columbia to southern Oregon, eastward across southern British Columbia to southwestern Alberta, south to northeastern Oregon, central Idaho and central Colorado. These subspecies are best defined by the ratio (PL/HW). The mean for samples (17) of the boreal subspecies is significantly smaller (mean range: 0.851 to 0.882 - average for all samples 0.864) than those (22) of the western subspecies (mean range; 0.884 to 0.916-average for all samples 0.896). The ranges of variation in means between samples show no geographical pattern for each subspecies. Based on above measurements, the two subspecies are characterized in a discriminant function allowing correct identification of 78% of individuals (Goulet and Baum, 1981). Moreover, the above function in combination with other characters mentioned below should allow correct identification of each specimen. Because the differences observed are maintained even when both subspecies are adjacent in their ranges, and because there is no clinal variation in character states studied, subspecific rank is given to these two populations. However, the results of various analyses clearly point out that *E. americanus* is probably a superspecies (Goulet and Baum, 1981) including two allopatric species, but more collecting is needed to determine rank of these taxa.

*Elaphrus americanus americanus* Dejean

Figs. 32, 34, 69a-c, 100a-b, 117, 128, 135, 170

*Elaphrus americanus* Dejean, 1831:558. Type locality: Great Bear Lake, Northwest Territories, subsequently designated by Lindroth (1961); type (seen by Lindroth) in Museum National d'Histoire Naturelle, Paris. Lindroth, 1961:115 (*ex parte*).

*Elaphrus intermedius* Kirby, 1837:62. Type locality: Great Bear Lake, Northwest Territories; type (seen by Lindroth) in British Museum of Natural History, London. Walker, 1866:309 (*ex parte*). Crotch, 1876:246; Schaupp, 1878:6. Lindroth, 1961:115.

*Elaphrus punctatissimus* LeConte, 1850:210. Type locality: Sault Ste. Marie, Michigan; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:401. Schaupp, 1878:6. Lindroth, 1961:115.

*Elaphrus sinuatus* LeConte, 1850:210. Type locality: Pic, Ontario (north shore of Lake Superior); type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:402. Lindroth, 1961:115.

*Elaphrus gratus* Mannerheim, 1853:118. Type locality: Kaktuu River, Kenai peninsula, Alaska; type (seen by Lindroth) in Zoological Museum, University, Helsinki. Schaupp, 1878:6. Lindroth, 1961:115.

*Elaphrus riparius*; Crotch, 1873:4 (*ex parte*). 1876:246 (*ex parte*). Schaupp, 1878:6 (*ex parte*). Taylor, 1886:35 (*ex parte*). Harrington, 1889:139 (*ex parte*). Venable, 1913:26 (*ex parte*). Hippius, 1922:63 (*ex parte*). Van Dyke, 1924:3. Guppy, 1947:51. Clark, 1948:25 (*ex parte*). Hatch, 1953:63 (*ex parte*). *nec* Linnaeus, 1758.

*Elaphrus bituberosus* Casey, 1924:17. Type locality: Terrace, British Columbia; lectotype (seen by me) designated by Lindroth (1976:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:115.

Table 33. Descriptive statistics for *E. americanus americanus*, based on 14 males and six females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.40–1.67	1.54	0.114	0.034	4.9
PW	1.52–1.82	1.64	0.147	0.044	6.0
EL	3.60–4.50	4.03	0.345	0.103	5.7
EW	1.35–1.70	1.48	0.152	0.045	6.8
HW	1.70–1.92	1.79	0.107	0.033	4.0
B. Proportions <sup>1</sup>					
PL/PW		0.936	0.043	0.013	3.1
PL/EL		0.382	0.019	0.006	3.4
PL/EW		1.040	0.068	0.020	4.3
PL/HW		0.862	0.031	0.009	2.4
PW/EL		0.408	0.020	0.006	3.3
PW/EW		1.110	0.054	0.016	3.2
PW/HW		0.922	0.037	0.011	2.7
EL/EW		2.720	0.110	0.033	2.7
EL/HW		2.250	0.106	0.032	3.1
EW/HW		0.831	0.053	0.016	4.3

<sup>1</sup>Values for "Range" not available.

## Adults

*Diagnostic combination.*— Recognized from adults of *E. americanus sylvanus* as follows: Accessory setae abundant on antennomere 3 (more than one seta per sample on average) and on metepisternum (few to numerous setae); pronotum relatively short (PL) and in combination with HW the ratio PL/HW smaller than 0.883 on average per sample (for discriminant function based on the same variables see Goulet and Baum, 1981); punctures of elytral intervals 4 dense (less than 40 microns apart on average per sample); foretibial sulcus (groove parallel to fringe) expressed in most specimens, but well developed in few; mirrors of elytron confluent in few specimens; apex of median lobes of males, in lateral view narrow, and in ventral view, straight (Figs. 69a, 69b).

*Description.*— Two color forms (in some samples intermediate known). For details see *E. lecontei* (p. 295).

Antennomere 3 of most specimens with accessory setae (Fig. 12). Frons without medial impression, and without accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and with accessory setae in many specimens. Abdominal sterna with numerous accessory setae between ambulatory setae and lateral punctate area; setae more numerous in males than in most females. Main mirror of elytron rectangular; one to three rows of mirrors or only main mirror sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

*Integument sculpture.* Punctures 25 microns in diameter on dorsal body surface, and 30 to 35 microns in diameter ventrally. Punctures 2 to 10 microns apart in elytral pits, 10 to 60 microns apart on intervals 4, 6 and 8, about 20 microns apart submedially and 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit of elytron with three to six concentric rows of punctures. Abdominal sternum 3 with 100 to 200 punctures on each side.

Microsculpture flat or absent from elytral intervals, pronotum and head; convex on thoracic pleura, and flat (with a few points in basal area) on abdominal sterna between ambulatory setae and punctate area.

*Male genitalia.* Apex of median lobe in ventral view thick-edged and straight, and in lateral view narrowly spatulate (Figs. 69a, 69b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a); lobe shorter between angular bend and apex (3.5 to 4.7 mm). Setae of parameres long (Fig. 69c).

*Measurements and proportions.*— Eighteen samples studied, and data for one presented in Table 33.

*Variation.*— Members of this subspecies appear homogeneous except for those in northwestern North America. Adults from this region are small in most measurements (see PL and PW in Goulet and Baum (1981) in Table 5), show a low ratio PL/PW (smaller than 0.405), have generally no foretibial sulcus, have dense punctures on elytral interval 4 (15 to 20 microns apart on average per sample studied), have many concentric rows of punctures (greater than 4.3 on average per sample studied) in the first pit near the suture, and have the accessory setae of abdominal sterna closer to the lateral punctate area. However, in most of these characters, samples from northern British Columbia, central and northern Alberta, and western Northwest Territories are intermediate between Beringian samples and those farther south. Therefore, I do not consider these populations as subspecifically distinct.

#### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by character combination in key.

#### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Seta VEMP-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AIM on terga abruptly short, at least on tergum 8. Antero-dorsal seta on epipleura very small on segments 8, or 7 and 8, and larger on anterior segments.

#### Second and Third Instar Larvae

*Description.*— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

#### Geographical Distribution and Affinities, and Notes

*Distribution.*— Transamerican in forested areas of boreal regions, but not reaching the Pacific coast except in southwestern Alaska (Fig. 1; see Goulet and Baum, 1981).

*Collecting notes.*— Adults are regularly found on wet beaches along slow meandering creeks. The beach is almost horizontal and consists of organic, coarse and quite firm soil. The surface is sun-exposed and sheltered from winds. This habitat is regularly found around beaver ponds.

*Taxonomic notes.*— Holotypes studied of conspecific forms mentioned above match typical specimens of this subspecies. I studied more than 2000 adults, and dissected more than 300 males. I examined five first instar, eight second instar, and five third instar larvae from George Lake, Alberta.

*Geographical affinities.*— The range of this subspecies overlaps widely those of *E. californicus* and *E. tuberculatus*, and marginally those of *E. ruscarius* and *E. finitimus*. I have often seen adults of *E. californicus* with those of this subspecies, but in all instances those of one species was overwhelmingly dominant. Once, I found adults of this subspecies, *E. californicus* and *E. lecontei* on the same beach where the three habitats were found within 10 m, but adults of each species remained mainly in their respective habitat.

Table 34. Descriptive statistics for *E. americanus sylvanus*, based on ten males and ten females from Pullman, Washington.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.85	1.69	0.134	0.040	5.3
PW	1.65–2.05	1.82	0.164	0.049	6.0
EL	3.80–4.65	4.27	0.344	0.102	5.4
EW	1.45–1.82	1.60	0.169	0.050	7.0
HW	1.75–2.00	1.88	0.115	0.034	4.1
B. Proportions <sup>1</sup>					
PL/PW		0.929	0.036	0.011	2.6
PL/EL		0.396	0.019	0.006	3.2
PL/EW		1.050	0.060	0.018	5.7
PL/HW		0.897	0.029	0.009	2.1
PW/EL		0.427	0.020	0.006	3.1
PW/EW		1.140	0.057	0.017	3.3
PW/HW		0.966	0.046	0.014	3.2
EL/EW		2.660	0.102	0.030	2.6
EL/HW		2.270	0.098	0.029	2.9
EW/HW		0.852	0.052	0.015	4.1

<sup>1</sup>Values for "Range" not available.

*Elaphrus americanus sylvanus* Goulet

Figs. 67a-b, 68a-b, 170

*Elaphrus americanus sylvanus* Goulet, in Goulet and Baum, 1981:2271. Type locality: Oregon, Coos Co., 16 mi. N of Powers; holotype (No. 18011) in the Canadian National Collection, Ottawa.

**Adults**

*Diagnostic combination.*— Distinguished from adults of *E. americanus americanus* as follows: Accessory setae few on antennomere 3 (less than two setae on average per sample) and on metepisternum (most specimens without setae); pronotum relatively long (PL) and in combination with HW the ratio PL/HW greater than 0.884 on average per sample (for discriminant function based on the same variables see Goulet and Baum, 1981). For populations adjoining the range of *E. americanus americanus* (southern British Columbia and Alberta), punctures of elytral interval 4 scattered (more than 40 microns apart on average per sample); foretibial sulcus (groove parallel to fringe) well developed in most specimens; mirrors of elytron generally more confluent. Apex of median lobe of males, in lateral view, narrow (Fig. 68b) (Pacific coast, Cascades, and western Oregon populations) or wide (Fig. 67b) (elsewhere), and in ventral view, straight (Fig. 68a) (Pacific coast, Cascades, and western Oregon populations – with occasional specimens in other populations) or slightly twisted (Fig. 67a) (other populations).

**Description.**— Similar to specimens of *E. americanus americanus* except the following. Color: as for *E. americanus americanus* except for dark specimens from Mount Hood, Oregon and northeastern Oregon with microsculptured and smooth surfaces black and punctures blue-green.

Antennomere 3 of most specimens without accessory setae. Elytral pits slightly to deeply impressed. Punctures 10 to 100 microns apart on intervals 4, 6 and 8. Apex of median lobe in ventral view slightly twisted or straight, and in lateral view widely to narrowly spatulate (Figs. 67a, 67b, 68a, 68b).

**Measurements and proportions.**— Twenty-two samples studied, and data for one presented in Table 34.

**Variation.**— Seven populations are recognized: Pacific coast, Cascades, Mount Hood, Willamette Valley, northern Great Basin, northeastern Oregon, and central Rocky Mountains. There is no evidence of clinal variation among them, and their status as species or subspecies is therefore uncertain. These populations are characterized in Goulet and Baum (1981).

### All Instar Larvae

**Diagnostic combination.**— The few specimens studied match those of *E. americanus americanus*.

### Geographical Distribution and Affinities, and Notes

**Distribution.**— In forested regions, from the Pacific coast along British Columbia to southern Oregon, eastward across southern British Columbia to southwestern Alberta, south to northeastern Oregon, central Idaho, and central Colorado. (Fig. 1; see Goulet and Baum, 1981).

**Collecting notes.**— In coastal Oregon, adults were found on clay beaches on the saturated portion. The habitat is similar to that of *E. californicus* except that adults run mostly on the saturated portion of the beach. However, in the Cascades, adults of the subalpine form are found in many localities running around snow surfaces on bare organic soil or on matted vegetation.

**Taxonomic notes.**— I studied about 1000 adults, and dissected more than 100 males. I examined one first instar and one third instar larva from Mount Rainier, Washington, and one third instar larva from the type locality near Powers, Oregon.

**Geographical affinities.**— The range of this subspecies overlaps widely with that of *E. californicus*, and marginally with those of *E. finitimus* and *E. marginicollis*.

### *Elaphrus comatus* new species

Fig. 63a-b

*Elaphrus riparius* Nakane, 1963:19. Ohkura, 1973:5. *nec* Linnaeus, 1758.

*Elaphrus comatus* new species. Type material: holotype male and allotype female labelled "No CHINA.; P.M. Hammond., B.M. 1967-215. Heilung kiang, Harbin, 12.6.66"; type deposited in British Museum (Natural History), London.

### Adults

**Diagnostic combination.**— Distinguished from adults of other Asiatic species by many long setae on dorso-apical surface of hind femur, and in lateral view by subtruncated apex of median lobe of males (Fig. 63b).

**Description.**— Only green specimens seen. For details about coloration see under *E. lecontei* (p. 295).

Antennomere 3 with few accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in situation, and not explanate before situation (Figs. 25, 77d); disc without or with one or two pairs of submedial impressions (Fig. 25). Abdominal sterna of both sexes with abundant accessory setae extended to edge of sterna 5 and 6. Main mirror of elytron rectangular; main mirror sharply outlined,

Table 35. Descriptive statistics for *E. comatus*, based on three males and six females from Japan (Muki) and China (Harbin).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.35–1.50	1.46	0.081	0.036	3.7
PW	1.55–1.70	1.61	0.081	0.036	3.4
EL	3.75–4.10	3.99	0.179	0.080	3.0
EW	1.42–1.62	1.54	0.106	0.047	4.6
HW	1.67–1.77	1.74	0.053	0.024	2.0
B. Proportions					
PL/PW	0.868–0.952	0.907	0.043	0.020	3.2
PL/EL	0.359–0.375	0.367	0.009	0.004	1.6
PL/EW	0.923–0.999	0.948	0.034	0.016	2.4
PL/HW	0.800–0.870	0.840	0.034	0.016	2.7
PW/EL	0.394–0.420	0.405	0.012	0.006	1.9
PW/EW	1.000–1.098	1.046	0.046	0.020	3.0
PW/HW	0.900–0.971	0.927	0.031	0.014	2.3
EL/EW	2.500–2.690	2.585	0.084	0.038	2.2
EL/HW	2.229–2.319	2.290	0.051	0.022	1.5
EW/HW	0.851–0.915	0.886	0.039	0.018	2.9

others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and impressed in basal half. Dorso-subapical surface of hind femur with many long (100 to 150 microns) setae (Fig. 35).

*Integument sculpture.* Punctures 20 to 25 microns in diameter on elytra, pronotum and head, 30 microns in diameter in elytral pits, and 30 to 35 microns in diameter on thoracic pleura. Punctures 10 to 20 microns apart on elytron, 5 to 10 microns apart in pits, 10 to 20 microns apart submedially and 30 to 50 microns apart laterally on pronotum, and 20 to 30 microns apart on proepisternum. First sutural pit of elytron with three to four concentric rows of punctures. Abdominal sternum 3 with 50 to 70 punctures on each side.

Microsculpture convex dorsally and absent in spots, convex on thoracic pleura, and flat on abdominal sterna (surface brilliant).

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view truncate (Figs. 63a, 63b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres long (Fig. 69c).

*Measurements and proportions.*— One sample studied, see Table 35.

*Variation.*— Samples from northeastern China and Japan appear similar. Unfortunately these samples are too small for analysis.

*Derivation of specific epithet.*— From Latin *comatus* meaning long-haired, referring to long setae on dorso-subapical surface of hind femur.

*Distribution.*— Known from northeastern China and Japan.

China. - HEILUNG KIANG: Harbin (7:BMNH).

Japan. - Muki (2:CASC)

*Geographical affinities.*— To my knowledge, the range of this species does not overlap with those of other species unless the range of *E. riparius* extends to the Pacific coast.

Table 36. Descriptive statistics for *E. riparius*, based on ten males and ten females from Silvakra, Skane, Sweden.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.30–1.67	1.51	0.126	0.038	5.6
PW	1.40–1.87	1.66	0.178	0.053	7.1
EL	3.30–4.25	3.92	0.332	0.099	5.6
EW	1.25–1.67	1.51	0.168	0.050	7.4
HW	1.60–1.97	1.77	0.144	0.043	5.4
B. Proportions					
PL/PW	0.840–0.953	0.909	0.039	0.012	2.9
PL/EL	0.371–0.400	0.384	0.012	0.004	2.1
PL/EW	0.940–1.067	1.002	0.054	0.016	3.6
PL/HW	0.812–0.877	0.849	0.025	0.008	2.0
PW/EL	0.401–0.446	0.423	0.018	0.003	2.8
PW/EW	1.050–1.167	1.103	0.045	0.014	2.7
PW/HW	0.875–1.000	0.935	0.040	0.012	2.9
EL/EW	2.476–2.755	2.606	0.120	0.036	3.1
EL/HW	2.062–2.313	2.209	0.091	0.028	2.8
EW/HW	0.781–0.893	0.848	0.042	0.012	3.3

*Elaphrus riparius* (Linnaeus).

Figs. 11, 25, 61a-b, 141, 143, 153

*Cicindela riparia* Linnaeus, 1758:407. Type locality: Uppsala, Sweden -- designated subsequently by Lindroth (1961); type (seen by Lindroth) in Linnean Collection, London. Poda, 1761:42. Müller, 1764:18, 178. De Geer, 1774:117. Müller, 1776:80, 864. Schrank, 1781:192. Thomson, 1859:3, 194.

*Elaphrus riparius*: Fabricius, 1775:227. Panzer, 1793:20. Illiger, 1798:225. Geoffroy, 1799:156 (*ex parte*). Fabricius, 1801:245. Latreille, 1804:217. 1806:227. 1810:425. Gyllenhal, 1810:6. Dejean, 1826:274. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Schiödte, 1841:356. Küster, 1846:7. Letzner, 1849:51. Fairmaire and Laboulbène, 1854:6. Schaum, 1856:72. Stierlin, 1869:11. Solsky, 1872:233. Redtenbacher, 1874:6. Seidlitz, 1875:2. Mäklin, 1877:17. Dalla-Torre, 1877:23. Sahlberg, 1880:10 (*ex parte*). Bedel, 1881:23. Fauvel, 1882:82, 84. Marseul, 1882:4. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:316. Everts, 1898:48. Semenov, 1904b:125. 1904a:20; Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhn, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Bänninger, 1919:148. Porta, 1923:78. Semenov, 1926:40. Portevin, 1929:41. Jacobson, 1931:82. Joy, 1932:328. Lindroth, 1939:62 - 67. Jeannel, 1941:217. Smetana, 1951:232. Lindroth, 1957:339. 1961: 115 (*ex parte*). 1974:33.

*Elaphrus paludosus* Olivier, 1790:5. Type locality: Paris, France; type not seen. Latreille, 1804:217. 1806:227. Dejean, 1826:274. Schaum, 1856:72. Marseul, 1882:4. Ganglbauer, 1892:123, 124. Semenov, 1895:315. 1904a:20. Jacobson, 1906:267. Jeannel, 1941:217.

*Elaphrus dilaticollis* R.F. Sahlberg, 1844:22. Type locality: Okhotsk Sea, USSR; type not seen. Marseul, 1880:31. 1882:4. Semenov, 1895:316. Jacobson, 1906:267.

*Elaphrus violaceomaculatus* Motschulsky, 1845:337. Type locality: Kamchatka, USSR; type not seen. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

*Elaphrus baschkiricus* Motschulsky, 1846:72. Type locality: Orenburg, Baschkir Aut Rep., USSR; type not seen. Marseul, 1882:4. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

*Elaphrus riparius* var. *nigrescens* Letzner, 1849:52. Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen. Jacobson, 1906:267.

*Elaphrus riparius* var. *viridis* Letzner, 1849:52. Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen.

Jacobson, 1906:267. Csiki 1927:92. Lindroth, 1961:110.

*Elaphrus riparius* var. *smaragdinus* Letzner, 1849:52 (name attributed to Müller, but to my knowledge never published). Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen. NEW SYNONYM.

*Elaphrus latiusculus* Motschulsky, 1850a:5. Type locality: Dauria (southeast of Lake Baikal), USSR; type not seen. Marseul, 1880:32. 1882:4. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

*Elaphrus riparius* var. *violaceomaculatus*; Marseul, 1882:4.

*Elaphrus californicus*; Ganglbauer, 1892:123. Semenov, 1895:315. 1904a: 20. Jacobson, 1906:267. Hatch, 1953:63. *nec* Mannerheim, 1843.

*Elaphrus punctatissimus*; Ganglbauer, 1892:123. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. Hatch, 1953:63. *nec* LeConte, 1850.

*Elaphrus intermedius*; Ganglbauer, 1892:123, 124. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* Kirby, 1837.

*Elaphrus similis*; Ganglbauer, 1892:123, 124. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* LeConte, 1848.

*Elaphrus sinuatus*; Ganglbauer, 1892:123, 124; Semenov, 1895:316. 1904a: 20. Jacobson, 1906:267. *nec* LeConte 1850.

*Elaphrus grattosus*; Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* Mannerheim, 1853.

*Elaphrus trosculus* Semenov, 1904a:21. Type area: Western Mongolia; type not seen. Jacobson, 1906:267. Bänninger, 1919:148 (suggested synonym).

*Elaphrus riparius* ab. *atratus* Wagner, 1917:259. Type locality: Brieslang, Germany; type not seen. Bänninger, 1919:148.

*Elaphrus riparius* ab. *cupritarsis* Bänninger, 1919:148. Type area: Turkestan; type does not exist. Name accidentally validated by Bänninger's discussion of Reitter's sample with the unpublished name attached to specimens.

*Elaphrus riparius* ab. *rubescens* Antoine, 1920:9. Type locality: between Berk-plage and Merlimont (Pas-de-Calais), France; type not seen.

*Elaphrus bituberosus*; Hatch, 1953:63 (*nec* Casey, 1924).

## Adults

**Diagnostic combination.**— Among species with expanded accessory setae on abdominal sterna, specimens of this species are separated from those of *E. parviceps* and *E. tibetanus* by more abundant punctures on abdominal sterna, and from those of *E. comatus* by shorter and fewer dorso-subapical setae on hind femur; they are separated from adults of *E. tuberculatus* with difficulty using the character combination in the key.

**Description.**— Two color forms: green and copper. For details see under *E. lecontei* (p. 295).

Antennomere 3 without accessory setae apically (Fig. 11). Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d), disc without or with one pair of weakly outlined submedial impressions, and with accessory setae on some specimens in central Asia. Abdominal sterna of both sexes with abundant accessory setae extended into lateral punctate area of segments 5 and 6. Main mirror of elytron rectangular; main mirror only, or mirror of first row, or exceptionally mirrors in two or three rows, sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

**Integument sculpture.** Punctures 20 to 25 microns in diameter on elytral intervals, pronotum and head, 30 microns in diameter on outer half of each elytral pit and abdominal sterna, and 30 to 40 microns in diameter on thoracic pleura. Punctures 5 to 10 microns apart in elytral pits, 10 to 20 microns apart on elytral intervals 4, 6 and 8, 15 to 20 microns apart submedially and 30 to 40 microns apart antero-laterally on pronotum, and 30 microns apart on proepisternum. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 50 to 80 punctures.

Microsculpture subconvex dorsally, convex in elytral pits, and on thoracic pleura, and forming sharp prominent scales between ambulatory setae and edge of abdominal sterna 5 and 6 in most specimens (best seen in diffused light, see Figs. 143 and 153).

**Male genitalia.** Apex of median lobe in ventral view edged and twisted, and in lateral view spatulate (Figs. 61a, 61b); base of lobe along angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61b). Setae of parameres long (Fig. 69c).

**Measurements and proportions.**— Three samples studied, and data for one presented in Table 36.

**Variation.**— As more material was needed, I did not attempt a detailed analysis of variation among populations of this species. However, the differences observed suggest a species complex. Specimens from southern Europe are generally golden green and dull, and those from western China and western USSR have accessory setae on the pronotum. In addition, as discovered by Smetana (1951), there is the possibility of isolated high altitude populations that may be in the process of differentiation (on this topic see Goulet and Baum, 1981). A study of this complex is



best suited for a student with access to large Palaearctic collections.

### All Instar Larvae

*Diagnostic combination.*— Recognized from larvae of other species by character combination in key.

### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum smooth. Epicranial suture 0.3 to 0.4 as long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AII and AIM on nota small. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleuron very small on segment 8, or on 7 and 8, and markedly larger on other segments.

### Second and Third Instar Larvae

*Description.*— Head brown behind eyes, and nota, terga and urogomphus dark brown.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— The range of this species extends into cold temperate and boreal regions of the Palaearctic Region, from the Atlantic coast as far east as western China, Mongolia and Lake Baikal. Records of this species along the Pacific coast probably refer to *E. comatus*. I have seen specimens from almost every European country reported by Lindroth (1945) and from central Asia.

*Collecting notes.*— Adults were collected on the moist and wet portions of sandy and clayish beaches along rivers, ditches, etc. Beaches were sun-exposed, and the vegetation scattered or absent. Adults are rarely found on organic, peaty, gravelly or rocky shores (Lindroth 1945).

*Taxonomic notes.*— The separation of adults of this species from those of *E. tuberculatus* is extremely difficult as pointed out by Lindroth (1939). I discovered independently the differences he observed, and confirmed his general conclusions. These differences are maintained across the range of both species. Moreover, larvae of *E. tuberculatus* (North American sample) and those of *E. riparius* (from Austria) are probably the most distinctive larvae of the subgenus. Therefore, I feel there is sufficient evidence to recognize *E. tuberculatus* as specifically distinct from *E. riparius*.

As no types were seen, the above synonymy is tentative. Based on descriptions of type series and their type localities, the following names are probably synonymous with *E. riparius*: *E. paludosus*, *E. baschkiricus* and *E. latiusculus*. Similarly, the following names are probably synonymous with *E. riparius*, and may represent only color variants: *E. riparius* var. *nigrescens*, *E. riparius* var. *viridis*, *E. riparius* var. *smaragdinus*, *E. riparius* ab. *atratus*, *E. riparius* ab. *cupritarsis* and *E. riparius* ab. *rubescens*. *E. riparius* ab. *atratus* may be a local color variant or a postmortem color change. Semenov (1895) suggested that *E. violaceomaculatus* and *E. dilaticollis* are synonymous with *E. riparius*. However, the type localities of these insects suggest perhaps a relation to the North American *E. tuberculatus* (see comments under this species). *E. trossulus*, based on Bänninger's specimens, represents a geographical variant of *E. riparius*. Bänninger's specimens fit Semenov's original (1904a) description perfectly.

I studied about 500 specimens, and dissected ten males. I examined three first instar, two second instar and three third instar larvae from Austria.

*Geographical affinities.*— The range of *E. riparius* overlaps those of *E. hypocrita* and *E. tuberculatus*.

Table 37. Descriptive statistics for *E. tuberculatus*, based on ten males and ten females from Sorcele, Sweden.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.67	1.53	0.100	0.030	4.3
PW	1.52–1.85	1.70	0.133	0.040	5.2
EL	3.75–4.50	4.17	0.283	0.084	4.5
EW	1.40–1.70	1.54	0.112	0.030	4.8
HW	1.67–1.97	1.82	0.112	0.034	4.1
B. Proportions					
PL/PW	0.811–0.954	0.904	0.051	0.016	3.8
PL/EL	0.333–0.390	0.368	0.022	0.006	4.0
PL/EW	0.882–1.050	0.992	0.054	0.016	3.6
PL/HW	0.759–0.875	0.841	0.042	0.012	3.3
PW/EL	0.387–0.432	0.407	0.017	0.006	2.7
PW/EW	1.048–1.167	1.098	0.040	0.012	2.4
PW/HW	0.871–0.986	0.931	0.040	0.012	2.9
EL/EW	2.623–2.807	2.698	0.081	0.024	2.0
EL/HW	2.143–2.417	2.289	0.111	0.032	3.2
EW/HW	0.800–0.880	0.849	0.035	0.010	2.7

*Elaphrus tuberculatus* Mäklin.

Fig. 171

*Elaphrus tuberculatus* Mäklin, 1877:16. Type locality: Brochowsky Island (70° 39' N) in Yenisey River, USSR; type not seen. Sahlberg, 1880:11. Jacobson, 1906:267. Semenov, 1909:433. Bänninger, 1919:148. Semenov, 1926:40. Bänninger, 1931:184.

*Elaphrus ripariensis* J. Sahlberg, 1880:10. Type locality: Dudinka, USSR; type not seen. Semenov, 1904a:20. Jacobson, 1906:267. Semenov, 1909:433.

*Elaphrus riparius*; Sahlberg, 1880:10 (*ex parte*). Lindroth, 1961:116 (*ex parte*). *nec* Linnaeus, 1758.

*Elaphrus latipennis* var. *orientalis* Semenov, 1904a:20. Type locality: Bulun (lower Lena River), USSR; type not seen. Jacobson, 1906:267. Semenov, 1909:433.

*Elaphrus latipennis* ab. *costulifer* Semenov, 1904b:125. Type area: Arctic region of Kanin and Kolgujev, USSR; type not seen. Semenov, 1904a:20. Jacobson, 1906:267.

*Elaphrus latipennis* ab. *normalis* Poppius, 1908:4. Type locality: not known to me; type not seen. Semenov, 1909:433.

*Elaphrus tuberculatus* ab. *costulifer*; Semenov, 1909:433.

*Elaphrus tuberculatus* var. *orientalis*; Semenov, 1909:433.

*Elaphrus tumidiceps* Munster, 1924:288. Type locality: Lakselv in Porsanger, Norway; type (seen by Lindroth) in Oslo, Norway. Bänninger, 1931:184; Lindroth, 1939:62 - 67.

*Elaphrus riparius tuberculatus*; Lindroth, 1939:62 - 67.

**Adults**

*Diagnostic combination*.— Distinguished from adults of *E. comatus*, *E. parviceps* and *E. tibetanus* by character combination described under *E. riparius*. This species is separated from *E. riparius* using character combination in key.

*Description*.— Two color forms. For details see *E. lecontei* (p. 295), except the following. Tibiae metallic on dorsal surface of most specimens.

Table 38. Descriptive statistics for *E. tuberculatus*, based on ten males and ten females from Inuvik, N.W.T.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.32–1.55	1.44	0.115	0.034	5.3
PW	1.45–1.72	1.60	0.121	0.036	5.1
EL	3.50–4.50	4.01	0.371	0.111	6.2
EW	1.37–1.65	1.50	0.119	0.036	5.3
HW	1.60–1.82	1.73	0.081	0.024	3.1
B. Proportions					
PL/PW	0.855–0.938	0.899	0.037	0.012	2.8
PL/EL	0.329–0.401	0.359	0.025	0.008	4.7
PL/EW	0.900–1.036	0.958	0.057	0.016	4.0
PL/HW	0.768–0.870	0.830	0.046	0.014	3.7
PW/EL	0.382–0.432	0.399	0.019	0.006	3.2
PW/EW	1.032–1.117	1.066	0.040	0.012	2.5
PW/HW	0.896–0.970	0.924	0.039	0.012	2.8
EL/EW	2.500–2.828	2.672	0.115	0.034	2.9
EL/HW	2.088–2.500	2.316	0.142	0.042	4.1
EW/HW	0.809–0.939	0.867	0.051	0.016	3.9

Antennomere 3 without or with accessory setae (Fig. 11 and 12). Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in situation, and not explanate before situation (Figs. 25 and 77d); disc without or with one pair of submedial impressions and with accessory setae in few specimens. Abdominal sterna in both sexes with abundant accessory setae extended to edge of sterna 5 and 6. Main mirror of elytron rectangular; mirrors of first two or three rows sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

*Integument sculpture.* Puncture diameter as for *E. riparius*, except 20 to 30 microns across dorsally. Punctures generally less dense than in *E. riparius*: 10 to 25 microns apart in first sutural pit of elytron, and 15 to 30 microns apart on intervals. First sutural pit of elytron with four or five concentric rows of punctures. Abdominal sternum 3 with 40 to 80 punctures on each side.

Microsculpture generally convex on dorsal and pleural surfaces (dull reflection), convex on abdominal sterna, and with or without raised sharp scales basally (rarely expanded as in *E. riparius*).

*Male genitalia.* In every detail as that of *E. riparius* (Figs. 61a, 61b, 69c).

*Measurements and proportions.*— Three samples studied, and data for two presented in Tables 37 and 38.

*Variation.*— Between northern Scandinavian and eastern Siberian samples, I observed few differences. In eastern Siberia, 10% of adults have accessory setae on the pronotum, most have some accessory setae on the antennomere 3, and punctures are large on the pronotum (about 30 microns in diameter). In Scandinavia, adults have no accessory setae on the pronotum or on antennomere 3, and punctures are small on the pronotum (about 25 microns in diameter). Many specimens of both regions are copper in color. In North America, adults differ in many characteristics from Palaearctic samples: no copper individuals, punctures dense (15 to 20 microns apart) on the pronotum submedially, and only mirrors of the first row, or the main mirror, sharply outlined. Adults of this species in the Nearctic region are strictly riparian while

those in the Palearctic region are not, as suggested by notes on habitat (Lindroth, 1939, 1945). Finally the Scandinavian sample has a significantly larger mean for ratio PL/EW than those of other two samples. The limited data suggest that *E. tuberculatus* is a complex of taxonomically distinct forms.

### All Instar Larvae

*Diagnostic combination.*— Recognized from larvae of other species by character combination in key.

### First Instar Larvae

*Description.*— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AIM on terga subequal. Antero-dorsal seta of abdominal epipleuron very small on segments 8, or 7 and 8, and markedly longer on other segments.

### Second and Third Instar Larvae

*Description.*— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

### Geographical Distribution and Affinities, and Notes

*Distribution.*— This is a Holarctic species found from northern Scandinavia to eastern Siberia in southern arctic regions of the Palearctic Region, and from Alaska to the MacKenzie River in subarctic regions of the Nearctic Region. North American localities are mapped in Fig. 171.

*Collecting notes.*— Lindroth (1945, 1961) described the habitat of Scandinavian specimens under *E. riparius*. North American specimens were found almost exclusively along large subarctic rivers on silt beaches south of the tree line, specifically in front of the willow zone where a dense carpet of *Equisetum fluviatile* grew. Specimens of this species of horsetail have few short side branches, thus leaving the silt beach mostly sun-exposed. Adults were not found on sun-exposed silt substrate inside the willows. I found numerous specimens on silt and organic beaches of a small water reservoir with artificially depressed water table. At this reservoir, *E. americanus* also occurred though more abundantly on organic beaches. This last species was not found near the river.

*Taxonomic notes.*— Adults of this species are very similar to those of *E. riparius*. The reasons for keeping both taxa specifically distinct are discussed under *E. riparius*. Based on description of adults and their type locality the following nominal forms are probably conspecific with *E. tuberculatus*: *E. latipennis*, *E. latipennis* ab. *costulifer* and *E. tumidiceps*. I did not find the original description of *E. latipennis* ab. *normalis*, but Semenov associated it with *E. tuberculatus*. *E. latipennis* var. *orientalis*, based on the description of puncture density, may be *E. riparius* or the North American *E. tuberculatus* (the type locality along the lower Lena River is reminiscent of the North American situation). Based on descriptions of the type series and on type localities of *E. violaceomaculatus* and *E. dilaticollis*, both in subarctic or arctic regions of the Pacific coast of Asia, these forms may belong to this species rather than to *E. riparius* as suggested by Semenov (1895) who saw original specimens of these species.

Table 39. Descriptive statistics for *E. parviceps*, based on ten males and ten females from Anderson River Delta, N.W.T.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.30–1.55	1.46	0.088	0.026	4.0
PW	1.37–1.77	1.61	0.145	0.043	6.0
EL	3.65–4.40	4.13	0.298	0.078	4.2
EW	1.42–1.60	1.53	0.070	0.021	3.0
HW	1.60–1.75	1.69	0.061	0.018	2.4
<b>B. Proportions</b>					
PL/PW	0.824–1.127	0.912	0.091	0.028	6.7
PL/EL	0.333–0.390	0.354	0.019	0.006	3.7
PL/EW	0.912–1.069	0.959	0.054	0.016	3.7
PL/HW	0.812–0.939	0.864	0.043	0.012	3.3
PW/EL	0.346–0.420	0.390	0.027	0.008	4.6
PW/EW	0.948–1.136	1.054	0.072	0.022	4.6
PW/HW	0.833–1.000	0.950	0.067	0.020	4.7
EL/EW	2.561–2.767	2.707	0.081	0.024	2.0
EL/HW	2.280–2.559	2.438	0.097	0.030	2.7
EW/HW	0.870–0.926	0.901	0.025	0.008	1.9

*Elaphrus parviceps* Van Dyke

Figs. 4, 12, 116, 129, 136, 142, 144, 171

*Elaphrus parviceps* Van Dyke, 1925:112. Type locality: Seward Peninsula, Alaska; type (seen by me) in California Academy of Sciences, San Francisco. Lindroth, 1961:116.  
*Elaphrus riparius*; Lindroth, 1961:116 (*ex parte*) *nec* Linnaeus, 1758.  
*Elaphrus americanus*; Judd, 1967:51 *nec* Dejean, 181.

**Adults**  
*Diagnostic combination*.— Separated from adults of most species by fewer punctures on each side of the abdominal sternum 3 (0 to 50). Similar to those of *E. tibetanus*, but separated by short sinuation on pronotum and large punctures in elytral pits (25 to 30 microns in diameter).

*Description*.— Two color forms. For details see *E. lecontei* (p. 295) except tibiae metallic on dorsal surface. Antennomere 3 with 10 to 20 accessory setae. Frons without medial impression or accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25 and 77d); disc with or without one pair of indistinctly outlined submedial impressions and, in most specimens, with accessory setae. Abdominal sterna in both sexes with abundant accessory setae extended laterally to edge of sterna 5 and 6. Main mirror of elytron rectangular; mirrors sharply outlined in first two or three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

*Integument sculpture*. Punctures 25 to 30 microns in diameter on elytral intervals, 30 microns in diameter in pits, 25 microns in diameter on head and pronotum, and 30 to 35 microns in diameter on proepisternum. Punctures 10 to 20 microns apart in elytral pits, 20 to 30 microns apart on intervals 4, 6 and 8, 10 to 30 microns apart submedially and 40 to 60 microns apart antero-laterally on pronotum, and 30 to 40 microns apart on proepisternum. First sutural pit of elytron with three to five concentric rows of punctures. Abdominal sternum 3 with 0 to 50 punctures (usually 20 or less).

Microsculpture granulate in elytral pits, granulate to subconvex dorsally, convex to subconvex on thoracic pleura and flat on abdominal sterna (surface quite brilliant).

*Male genitalia.* As in *E. riparius* (Figs. 61a, 61b, 69c).

*Measurements and proportions.*— Four samples studied, and data for one presented in Table 39.

*Variation.*— Specimens from Alaska have a brighter surface and sparser punctures than those east of Alaska. Otherwise, no other differences were observed between above samples.

*Distribution.*— Known along southern arctic regions from the western shore of Hudson Bay to Commander Islands (U.S.S.R.). North American localities are mapped in Fig. 171.

*Collecting notes.*— Adults were found commonly on shores of small lakes and ponds, but not along shores of rivers, though these ponds were close to rivers (Ball pers. comm.).

*Taxonomic notes.*— I examined about 250 specimens, and dissected six males. The presence of this species on the Commander Islands suggests almost certainly its presence on Kamchatka and easternmost Siberia. Therefore, possibly the names *E. dilaticollis* and *E. violaceomaculatus*, synonymized under *E. riparius* by Semenov, (1895) may refer to this species.

*Geographical affinities.*— The range of *E. parviceps* is adjacent to ranges of the related species *E. americanus* and *E. tuberculatus*. Only few specimens of *E. parviceps* were found in the range of the latter two species.

### *Elaphrus tibetanus* Semenov

*Elaphrus tibetanus* Semenov, 1904a:22. Type area: Eastern Tibet, China, type not seen but specimens from original series seen.

### Adults

*Diagnostic combination.*— Similar to adults of *E. parviceps*, and distinguished as follows: pronotum with longer sinuation, punctures small (20 microns in diameter) in elytral pits and large (25 microns in diameter) on pronotum.

*Description.*— Two color forms: green and copper. For details see *E. lecontei* (p. 295) except tibiae metallic on dorsal surface.

Antennomere 3 with 10 to 20 accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex and elongate, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc without or with one pair of indistinctly outlined submedial impressions, and with accessory setae in most specimens. Abdominal sterna of both sexes with abundant accessory setae extended laterally in punctate area. Main mirror of elytron rectangular; mirrors sharply outlined in first two or three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and very slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

*Integument sculpture.* Punctures 20 microns in diameter in elytral pits, 25 microns in diameter on pronotum, and 30 microns in diameter on proepisternum. Punctures 20 to 30 microns apart in elytral pits, 10 to 20 microns apart in intervals 4, 6 and 8 and on pronotum submedially, 40 microns apart antero-laterally on pronotum, and 20 to 30 microns apart on proepisternum.

Microsculpture granulate on most of dorsal surface, convex on thoracic pleura, and flat on abdominal sterna (surface brilliant).

*Male genitalia.* Median lobe not associated with dissected male. Palmén (1944:21) figured the lobe in lateral aspect; the apex seems shorter and wider than in *E. riparius*, and setae of paramere seem short.

*Measurements and proportions.*— Based on two specimens from the Basin of the Yellow River, China. PL, 1.3-1.3 mm; PW, 1.4-1.6 mm; EL, 3.4-3.5 mm; EW, 1.2-1.4 mm; HW, 1.4-1.6 mm; PL/PW, 0.84-0.91; PL/EL, 0.37-0.39; PL/EW, 0.95-1.08; PL/HW, 0.82-0.91; PW/EL, 0.42-0.44; PW/EW, 1.12-1.18; PW/HW, 0.97-1.00; EL/EW, 2.56-2.80; EL/HW, 2.21-2.36; EW/HW, 0.84-0.86.

*Variation*.— Only two adults studied, thus not discussed.

*Distribution*.— Known from eastern Chinese highlands; for details see Semenov (1904a). I have seen two adults out of 55 seen by Semenov from the valley of Dzatshu River and Sergtshu in the Yellow River Basin.

*Collecting notes*.— Collected by the Koslov expedition from late April to July 1901 at various proximate locations between 11,000' and 14,000' (Russian feet) above sea level.

*Geographical affinities*.— The present range of this species does not overlap those of other species.

## SPECIES OF UNKNOWN STATUS

### *Elaphrus smaragdiceps* Semenov

*Elaphrus smaragdiceps* Semenov 1889:354. Type locality: Dshoni (8,820 ') in Amdo Mountains, Kansu, China; type not seen. Semenov 1904a:19. 1904b:125.

*Taxonomic notes*.— The type series belongs to subgenus *Elaphrus* as the prosternum is pubescent and only the three basal tarsomeres of forelegs of males have spongy pubescence (Semenov, 1904a).

The following character combination suggests that Semenov's species is probably distinct. I cannot include it in my key as many important characters were not observed by Semenov. The following characters were judged potentially more significant: pronotum longer than wide, lateral margin slightly convex and sinuation elongate; lateral margin of elytra markedly constricted in basal 0.3, only mirrors in first row clearly outlined; tibiae red-brown, but metallic at base and apex.

The male seems to have elytra as in adults of *E. californicus*, and body features like those of *E. ulrichi*. The color peculiarities (bright green head and pronotum and copper elytra) may be aberrant as suggested by Semenov (1904): "*capite majore ex parte smaragdino-viridi, semperne?*", though it matches that of the bicolor form of *E. californicus*. Among known Palaearctic species, the male of this species is the only one with very constricted elytra. Lindroth (1961) illustrates the constriction of *E. californicus* in Fig. 57b. Other characteristics, though interesting, are variable, and should be used with care.

### *Elaphrus irregularis* Scudder

*Elaphrus irregularis* Scudder, 1890. Type locality: Scarborough, Toronto, Ontario; type seen in the Museum of Comparative Zoology, Cambridge, Massachusetts.

*Taxonomic notes*.— The fossil elytron is in poor condition. However, sculpture, mirrors and pits clearly associate the type with members of subgenus *Elaphrus*. It is not *E. ruscarius* (larger elytral punctures than those on the fossil), nor *E. californicus* (denser punctures on elytra than those on the fossil), nor *E. tuberculatus* of North America (mirrors with some meshes of microsculpture, absent from the fossil). Character states on fossils match either *E. americanus* or *E. parviceps*, being in the range of overlap between these two species. The following combination of characters would suggest a match with *E. parviceps*: punctures spaced in elytral pits near main mirror (two or three microsculpture meshes between punctures), and in interval 1 and 2; punctures generally large (30 microns in diameter) in elytral pits near main mirror, and on intervals 1 and 2; microsculpture convex over most of surface except on mirrors. Since the type is in poor condition, and *E. parviceps* and *E.*

*americanus* are known from fossil samples at the type locality, I prefer to leave *E. irregularis* as incertae sedis.

### Subgenus *Elaphroterus* Semenov

*Elaphroterus* Semenov, 1895:309, 313. Type-species: *Elaphrus aureus* Müller, 1821, fixed by Semenov (1926), by subsequent designation. Semenov, 1904a:19 (*ex parte*). Jacobson, 1906:267 (*ex parte*). Reitter, 1908:96, 97 (*ex parte*). 1909:104 (*ex parte*). Bänninger, 1919: 149 (*ex parte*). Porta, 1923:78 (*ex parte*). Semenov, 1926:39. Portevin, 1929:41 (*ex parte*). Jeannel, 1941:216. Hatch, 1953:63. Ball, 1960:106. Lindroth, 1961:119. Nakane, 1963:19.

*Elaphrotatus* Semenov, 1895:308. Type-species: *Elaphrus punctatus* Motschulsky, 1846, fixed by Semenov (1926), by subsequent designation. Jacobson, 1906:268. Semenov, 1926:39. NEW SYNONYM.

### Adults

**Diagnostic combination.**— Distinguished from adults of other subgenera as in following. Fringe of setae along posterior margin of pronotum extended to hind angles. Disc of prosternum and process of mesosternum asetose. Trochanter of foreleg with two setae. Trochanter of midleg with one or two setae. Setae on inner 0.5 of hind coxa.

**Description.**— *Head.* Frons without medial impression, Clypeus with one pair of setae. Terebral margin of right mandible more than 0.5 as long as mandible; basal retinacular tooth entire, and apex of retinacular tooth near terebral tooth. Maxillary palpomere 3, 0.3 length of palpomere 4. Galeomere 1, 1.5 length of maxillary palpomere 2.

*Thorax.* Lateral margin of pronotum beaded except in situation, or unbeaded. Fringe of setae along posterior margins of pronotum extended to hind angles; setae scimitar-shaped and moderately expanded apically. Prosternum without setae or with a few setae on prosternal process. Mesosternal process without setae; postero-lateral ridge of mesosternum absent.

*Abdomen.* Tergum 7 without setae except on stridulatory scraper plates.

*Elytra.* Striae lacking. Transverse basal stria indistinctly outlined at shoulder. Setigerous punctures of elytra 40 to 50 microns in diameter. Interval 3 with one to three wide mirrors (Fig. 116). Elytral pits with 25 punctures or more, punctures regularly distributed (Figs. 124, 125).

*Legs.* Foreleg: trochanter with two setae; femur with 35 to 50 setae; tibia with 17 to 27 setae; inner dorsal fringe of setae 0.7 as long as tibia, and without setae posteriorly; first three tarsomeres of males with spongy pubescence ventrally, or pubescence lacking. Midleg: trochanter with one or two setae; femur with 35 to 50 setae; tibia with about 70 setae. Hindleg coxa with three to 20 setae on inner half. Femur with 18 to 21 setae; tibia with 65 to 80 setae.

*Male genitalia.* Internal sac of median lobe without large scales basally.

*Ovipositor.* Basal sclerite of stylus without apico-ventral setae; apical sclerite without setae (Fig. 74).

### All Instar Larvae

**Diagnostic combination.**— Distinguished from larvae of other subgenera as in following. Seta EA-E on frontale small. Epicranial suture 0.7 or less as long as antennal scape. Outer surface of stipes with membranous declivity behind postero-lateral seta, outer margin projected outward at declivity; postero-ventral pores proximate (Fig. 83b).

### First Instar Larvae

**Description.**— Medial point of nasale acute; teeth of nasale slightly coarser than in larvae of subgenus *Elaphrus*, and ending at base of medial point (Fig. 92). Seta EA-E of frontale small. Epicranial suture less than 0.7 as long as antennal scape. Head short: bisinuation of lateral margin behind eye with anterior and posterior convexity subequal. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 90° to 110°. Triangle formed by setae DEP, VEM-P and VEP-P on parietale short (anterior angle open). Pointed microsculpture on 2 to 25% of ventral surface of parietale. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin of stipes projected outward; dorsal surface of stipes with 40 to 50 setae on inner half, subapical setae roughly distributed in two to five rows; postero-ventral pores of stipes proximate (Fig. 83b). Pronotum with meshed microsculpture on 60% of surface, pointed microsculpture lacking. Pointed microsculpture on entire surface of anterior band of terga 1 to 8.



## Second Instar Larvae

**Description.**— Outer margin of stipes behind postero-lateral seta protruded. Each sclerite of pronotum and of mesonotum with 20 to 40 accessory setae; pointed microsculpture on entire anterior band surface. Each sclerite of terga 1 to 8 with 16 to 28 accessory setae. Basal accessory seta of urogomphus dorso-medially; pointed microsculpture on entire anterior band of terga 1 to 9, and on entire posterior band of terga 1 to 8. Hypopleuron of segments 1 to 8 with about four accessory setae.

## Third Instar Larvae

**Description.**— Surface of proepisternum with 10 accessory setae. Each sclerite of mesonotum with 30 to 55 accessory setae, mesonotal epipleuron with one to five accessory setae. Mesepimeron with two accessory pores or less. Largest projection of urogomphus in lateral view suggested or small. Sclerites of terga 1 to 8 each with 40 to 55 accessory setae. Epipleuron of abdominal segments 2 to 8 with 17 to 40 accessory setae. Hypopleuron of abdominal segments 1 to 8 with 12 to 22 accessory setae. Sternite of segment 1 with 14 to 18 accessory setae, that of segments 2 to 7 each with 25 to 40, that of segment 8 with 25 to 40, that of segment 9 with four to 12, and that of segment 10 with five to 12. Inner poststernites with two to five accessory setae.

## Geographical Distribution and Affinities, and Notes

**Distribution.**— The range of species of this subgenus extends across the Palaearctic Region and the western portion of the Nearctic Region, from the subarctic to the warm temperate zone.

## Key to the species and subspecies of subgenus *Elaphroterus* Semenov

### Adults

- 1 Dorsal surface with faint brassy hue. Punctures of pronotum 45 microns in diameter. Trochanter of midleg with two setae. Eastern Asia ..... *E. punctatus* Motschulsky p. 326
- 1' Dorsal surface metallic green, gray-green or copper. Punctures of pronotum 30 microns in diameter. Trochanter of midleg with one seta ..... 2
- 2 (1') Lateral margin of pronotum beaded, bead extended along most of margin except in situation. Intercoxal process of prosternum of many specimens with one or two accessory setae. Cold temperate regions of Europe, isolated in Caucasus Mountains ..... *E. aureus* Müller p. 328
- 2' Lateral margin of pronotum rounded, angular or barely beaded at middle. Intercoxal process of prosternum without accessory setae ..... 3
- 3 (2') Lateral margin of pronotum rounded or barely angulate near middle (Fig. 27). Femur testaceous, except for two metallic green spots, one medially and one apically. Tibia of foreleg of male with large sharp projection at base of posterior spur --best seen in posterior view of tibia (Fig. 149). Western Nearctic Region ..... *E. purpurans* Hausen p. 330
- 3' Lateral margin of pronotum angular to great extent (Fig. 26). Femur red-brown or piceus except for metallic green dorsal surface. Tibia of foreleg of male without projection at base of posterior spur. Palaearctic or northwestern Nearctic Regions ..... 4
- 4 (3') Pronotum with many bright copper reflecting surfaces. Dorsal body surface bright due to lack of, or presence of flat microsculpture. Hind angle of pronotum without proximal setigerous puncture. Dorsal surface of head,

- pronotum and side of elytron brilliant metallic golden-green. Elytron with one or two rows of indistinctly outlined mirrors. Accessory setae absent from posterior surface of metasternum. Middle Europe ..... *E. ulrichi* Redtenbacher p. 338
- 4' Pronotum, at most, with dark copper reflecting surfaces. Dorsal body surface dull, due to convex microsculpture. Hind angle of pronotum with proximal setigerous puncture. Dorsal surface dull green, grey-green, bluish green, or copper. Elytron with three rows of distinctly outlined mirrors (Fig. 116). Accessory setae on posterior surface of metasternum. Boreal and subarctic regions of Palaearctic and Nearctic Regions ..... 5
- 5 (4') Dorsal surface of elytron relatively smooth: pits little impressed and mirrors flat. Punctures in intervals 4, 6 and 8, in most specimens 30 to 40 microns apart. Pronotum without accessory setae. Coxa of hind legs with two to five accessory setae. Metasternum without accessory setae laterally. Abdominal sterna 4, 5 and 6 with one to eight accessory setae. Color: bluish-gray dorsally with green legs. West of Yenisey River ..... *E. angusticollis longicollis* Sahlberg p. 336
- 5' Dorsal surface of elytron relatively coarse: pits more deeply impressed and mirrors convex (Fig. 116). Punctures on intervals 4, 6 and 8, in most specimens 10 to 20 microns apart (Fig. 125). Pronotum of 50% of specimens with accessory setae. Coxa of hind leg with 10 to 20 setae. Metasternum with many accessory setae laterally. Abdominal sterna 4, 5 and 6 with 10 to 20 accessory setae. Color: green dorsally with green legs, or gray-green dorsally with copper femur and clypeus, or red-copper dorsally except for gray-green sutural and apical area of elytra. East of Lena River and in Northwestern portion of Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334

First Instar Larvae.

- 1 Epicranial suture short: 0.25 as long as antennomere 1. Apical inner margin of mandible and posterior edge of retinaculum distinctly toothed. Pointed microsculpture absent from latero-ventral surface of parietale. Europe ..... *E. aureus* Müller p. 328
- 1' Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Apical inner margin of mandible and posterior margin of retinaculum smooth or indistinctly toothed. Pointed microsculpture on 5% or more of latero-ventral surface of parietale ..... 2
- 2 (1) Seta MP and EM-P of frontale barely suggested or absent. Pointed microsculpture of parietale restricted latero-ventrally (5% of surface), and absent latero-dorsally Western Nearctic Region. .... *E. purpurans* Hausen p. 330
- 2' Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread latero-ventrally (20% or more of surface) and latero-dorsally (10% or more of surface) ..... 3
- 3 (2') Parietale dark brown only near frontale and epicranial suture.

Microsculpture of abdominal terga single-pointed. Pointed microsculpture well developed near sutural portion of mesonotum and metanotum. East of Lena River and in western Nearctic Region .....

..... *E. angusticollis angusticollis* Sahlberg p. 334

- 3' Parietale dark brown except behind eyes and along base. Microsculpture of abdominal terga multi-pointed. Pointed microsculpture absent from sutural portion of mesonotum and metanotum. Middle Europe .....

..... *E. ulrichi* Redtenbacher p. 338

## Second Instar Larvae

- 1 Epicranial suture short: 0.25 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 20 accessory setae. Pointed microsculpture absent from parietale baso-laterally. Europe .....

..... *E. aureus* Müller p. 328

- 1' Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 40 accessory setae. Pointed microsculpture well developed on parietale baso-laterally ..... 2

- 2 (1') Seta MP and EM-P of frontale absent. Pointed microsculpture of parietale restricted to latero-ventral portion (5% of ventral surface). Urogomphus, with only medium-sized and large accessory setae. Main accessory setae of hypopleura 1 to 8 large. Western Nearctic Region .....

..... *E. purpurans* Hausen p. 330

- 2' Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread on latero-ventral portion (15% or more of ventral surface). Urogomphus, in addition to medium-sized and large accessory setae, with numerous very small ones. Main accessory setae of hypopleura 1 to 8 small ..... 3

- 3 (2') Parietale dark brown only near frontale and epicranial sutures; nota and terga brown. Microsculpture of abdominal terga single-pointed. Largest projection of urogomphus clearly outlined (Fig. 101a). East of Lena River and in western portion of Nearctic Region .....

..... *E. angusticollis angusticollis* Sahlberg p. 334

- 3' Parietale dark brown except behind eyes and along base; pronotum, tergum 1 and outer third of terga 2 to 8 red-brown, and mesonotum, metanotum and inner two thirds of terga 2 to 8 and tergum 9 dark brown. Microsculpture of abdominal terga multi-pointed. Largest projection of urogomphus in lateral view no more than barely outlined. Middle Europe .....

..... *E. ulrichi* Redtenbacher p. 338

## Third Instar Larvae.

- 1 Epicranial suture short: 0.25 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 30 accessory setae. Pointed microsculpture of parietale absent laterally. Europe .....

..... *E. aureus* Müller p. 328

- 1' Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Each sclerite of mesonotum and metanotum with 50 or more accessory setae. Pointed microsculpture of parietale well developed laterally ..... 2
- 2 (1') Setae MP and EM-P of frontale absent. Pointed microsculpture of parietale restricted to latero-ventral portion (5% of surface). Urogomphus with only medium-sized and large accessory setae. Main accessory setae on hypopleura 1 to 8 large. Lateral band of pronotum without microsculpture. Western Nearctic Region ..... *E. purpurans* Hausen p. 330
- 2' Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread on latero-ventral portion (15% or more of surface). Urogomphus with numerous very small accessory setae in addition to medium-sized and large ones. Main accessory setae on hypopleura 1 to 8 small. Lateral band of pronotum with pointed microsculpture ..... 3
- 3 (2') Parietale dark brown only near frontale and epicranial suture; nota and terga dark brown. Microsculpture of abdominal terga single-pointed. Largest projection of urogomphus in lateral view about 0.5 as wide as urogomphus below. East of Lena River and in western portion of Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334
- 3' Parietale dark brown except behind eyes and along base; pronotum, tergum 1 and outer 0.3 of terga 2 to 8 red-brown, and mesonotum, inner 0.7 of terga 2 to 8 and tergum 9 dark brown. Microsculpture of abdominal terga multi-pointed. Largest projection of urogomphus in lateral view no more than barely outlined. Middle Europe ..... *E. ulrichi* Redtenbacher p. 338

*Elaphrus punctatus* Motschulsky

Figs. 53a-c, 54a-b, 112, 124

*Elaphrus punctatus* Motschulsky, 1846:73. Type locality: Lake Baikal USSR; type not seen. Sahlberg, 1880:10. Marseul, 1882:4. 1881:67. Jacobson, 1906:268. Nakane, 1955:22. Nakane *et al.*, 1963:19. Ohkura, 1973:6.

*Elaphrus cribratus* Semenov, 1889:353. Type locality: China, Szetschuan in mountains of Amdo, 6000'; type not seen. Jacobson, 1906:268. (suggested synonym).

## Adults

**Diagnostic combination.**— Distinguished from adults of other species by large punctures (30 to 60 microns), by almost black dorsal surface of body with weak metallic reflections, and by presence of four to six accessory setae on prosternal process and of two setae on trochanter of midleg.

**Description.**— Dorsal and ventral surfaces almost black with very weak green and copper reflections. Legs and mouthparts dark brown with weak metallic green reflections.

Antennomere 4 densely pubescent in apical 0.5. Pronotum with lateral margin very thinly and apparently completely beaded, with setigerous puncture near hind angle, and with one pair of submedial impressions. Prosternal process with four to six accessory setae. Accessory setae of metasternum present anteriorly, posteriorly and laterally. Abdominal sterna 4, 5 and 6 with more than ten accessory setae. Elytral mirrors flat, in three rows; sutural mirrors subequal in width. Elytral pits not impressed and not sharply outlined. Males without secondary sexual characters (first three tarsomeres of foreleg without spongy pubescence, tarsomeres narrow, and tibia of midleg without projection at base of inner spur). Trochanter of midleg with two setae, and coxa of hindleg with about 15 accessory setae. Tibia of foreleg without projection at base of posterior spur.

**Integument sculpture.** Punctures 30 microns in diameter on elytral intervals 4, 6 and 8, 40 to 50 microns in diameter on head, pronotum and elytral pits, and 50 to 60 microns in diameter ventrally. Punctures 10 to 20 microns apart

Table 40. Descriptive statistics for *E. punctatus*, based on six males and three females from USSR (Irkutsk), Japan (Ibaragi, Pref., Sairama), and China (northern China, Kuku-nor).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.32–1.57	1.50	0.121	0.054	5.3
PW	1.40–1.72	1.58	0.155	0.069	6.5
EL	3.30–4.02	3.70	0.372	0.165	6.7
EW	1.22–1.70	1.38	0.216	0.096	10.4
HW	1.67–1.95	1.82	0.130	0.058	4.7
B. Proportions					
PL/PW	0.912–0.999	0.952	0.043	0.020	3.0
PL/EL	0.385–0.449	0.407	0.028	0.012	4.7
PL/EW	0.779–1.224	1.098	0.199	0.088	12.1
PL/HW	0.791–0.873	0.826	0.037	0.016	3.0
PW/EL	0.404–0.464	0.427	0.025	0.012	4.0
PW/EW	0.824–1.255	1.153	0.195	0.086	11.3
PW/HW	0.836–0.901	0.868	0.033	0.014	2.5
EL/EW	1.941–2.980	2.700	0.442	0.196	10.9
EL/HW	1.944–2.137	2.034	0.087	0.038	2.8
EW/HW	0.690–1.015	0.762	0.147	0.066	12.9

submedially; 20 to 30 microns apart laterally on pronotum and 20 microns apart on elytral intervals 4, 6 and 8.

Microsculpture over most of dorsal body surface except of frons and elytral mirrors, more convex in elytral pits, and subconvex elsewhere; microsculpture of ventral body surface weakly outlined on most of abdominal sterna, elsewhere flat or absent in spots.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and strongly twisted (Fig. 54a), and in lateral view short and subtruncate (Fig. 53a and 54b). Setae of parameres long (Fig. 53c).

*Measurements and proportions.*— One sample studied. See Table 40.

*Variation.*— Despite a small sample from a large area, I observed striking structural differences. Specimens from Lake Baikal, USSR and Kuku-nor, China (Tibet) have indistinctly outlined and contrasted mirrors on elytron against the bright intervals 4, 6 and 8 (microsculpture absent or barely suggested, and punctures irregularly distributed on these intervals). However, specimens from Japan and Northern China have sharply outlined and contrasted mirrors against dull intervals 4, 6 and 8 (microsculpture subconvex, and regularly distributed on these intervals).

*Distribution.*— I have seen specimens from Irkutsk (near Lake Baikal), USSR; Kuku-nor, 3200 m, China (Tibetan region); northern China; Honshu and Hokaido Islands, Japan.

*Taxonomic notes.*— The descriptions of *E. cribatus* and *E. punctatus* are similar and match available specimens. The specimens from Lake Baikal and Kuku-nor are near the type locality of each taxon. Since adults from these two localities are similar, I feel these two names refer to one form of one species.

I studied nine specimens and dissected two males.

*Geographical affinities.*— The range of this species is isolated from any other species of this subgenus.

Table 41. Descriptive statistics for *E. aureus*, based on ten males and ten females from Austria (Graz, Wien) and Switzerland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.52–1.77	1.61	0.108	0.032	4.5
PW	1.62–1.90	1.74	0.109	0.033	4.2
EL	3.65–4.15	4.00	0.211	0.063	3.6
EW	1.40–1.60	1.49	0.085	0.026	3.8
HW	1.67–2.07	1.96	0.098	0.029	3.3
B. Proportions					
PL/PW	0.886–0.972	0.952	0.036	0.010	2.6
PL/EL	0.387–0.428	0.409	0.018	0.006	2.9
PL/EW	1.033–1.143	1.084	0.039	0.012	2.4
PL/HW	0.787–0.855	0.820	0.028	0.008	2.3
PW/EL	0.419–0.466	0.441	0.021	0.006	3.2
PW/EW	1.117–1.232	1.170	0.048	0.014	2.7
PW/HW	0.848–0.916	0.885	0.031	0.010	2.4
EL/EW	2.594–2.733	2.654	0.057	0.016	1.4
EL/HW	1.921–2.078	2.009	0.061	0.018	2.0
EW/HW	0.737–0.779	0.757	0.019	0.006	1.7

*Elaphrus aureus* Müller

Figs. 55a-c, 101a-b

*Elaphrus aureus* Müller, 1821:229. Type locality: not given; type not seen. Herr, 1838:39. Motschulsky, 1846:72. Küster, 1846:7. Letzner, 1849:52. Chaudoir, 1850:161. Fairmaire and Laboulbène 1854:6. Schaum, 1856:74. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Fauvel, 1882:82, 84. Marseul, 1882:4. Reitter, 1887:16. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:305. 1897:596. Everts, 1898:49. Jacobson, 1906:267. Semenov, 1907:259. Reitter, 1908:96, 97. 1909:106. Kuhnt, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Bänninger, 1919:149. Porta, 1923:78. Semenov, 1926:40. Portevin, 1929:41. Jeannel, 1941:217.

*Elaphrus littoralis* Dejean, 1826:275. Type area: Ukraine, Hungary and Austria; type not seen. Erichson, 1837:4. Heer, 1838:39. Motschulsky, 1846:73. Küster, 1846:7. Letzner, 1849:52. Chaudoir, 1850:161. Fairmaire and Laboulbène 1854:6. Schaum, 1856:74. Stierlin, 1869:11. Marseul, 1882:4. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Everts, 1898:49. Jacobson, 1906:267. Bänninger, 1919:149. Jeannel, 1941:217.

*Elaphrus smaragdinus* Reitter, 1887:16. Type locality: Czechoslovakia, near Paskov on shore of Ostravice River; type not seen. Ganglbauer, 1892:123, 124. Semenov, 1895:306. Gerhardt, 1899:14. Semenov, 1907:259.

*Elaphrus smaragdinus*; Jacobson, 1906:267.

*Elaphrus tschitscherini* Semenov, 1897:595. Type area: Caucasus, USSR; type not seen. Jacobson, 1906:268.

*Elaphrus aureus* var. *smaragdinus*; Reitter, 1908:96, 97. 1909:106. Kuhnt, 1912:50. Schaufuss, 1916:29.

*Elaphrus tchitcherini*; Semenov, 1926:40 (invalid emendation).

**Adults**

*Diagnostic combination.*— Distinguished by beaded lateral margin of pronotum from other metallic species of this subgenus.

*Description.*— Dorsal surface gray-green. Microsculptured surfaces brass or weakly copper colored; punctures green or blue-green; elytral pits purple near setigerous puncture. Femur dark brown underneath and metallic above.

Table 42. Descriptive statistics for *E. aureus*, based on five males and three females from Caucasus Mountains, USSR (Taberda, Kislovodsk).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.37–1.57	1.52	0.099	0.047	4.3
PW	1.57–1.75	1.65	0.094	0.044	3.8
EL	3.75–4.10	3.88	0.195	0.092	3.3
EW	1.30–1.50	1.42	0.110	0.052	5.2
HW	1.77–1.97	1.88	0.112	0.053	3.9
B. Proportions					
PL/PW	0.846–0.954	0.919	0.055	0.026	4.0
PL/EL	0.367–0.406	0.392	0.018	0.008	3.1
PL/EW	1.033–1.154	1.071	0.060	0.028	3.7
PL/HW	0.775–0.833	0.808	0.028	0.014	2.4
PW/EL	0.417–0.439	0.426	0.013	0.006	2.1
PW/EW	1.121–1.226	1.166	0.060	0.028	3.4
PW/HW	0.844–0.915	0.879	0.030	0.014	2.4
EL/EW	2.632–2.885	2.735	0.126	0.060	3.1
EL/HW	1.987–2.130	2.062	0.072	0.034	2.3
EW/HW	0.722–0.781	0.754	0.030	0.014	2.8

Antennomere 4 densely pubescent in apical 0.5. Pronotum with lateral margin clearly beaded except in sinuation, with setigerous puncture near hind angle of pronotum, and with one pair of submedial impressions. Prosternal process with fewer than three accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal sterna 4, 5 and 6 with three to six accessory setae. Elytral mirrors in two rows, clearly outlined, and convex; first or first and third sutural mirrors wider. Elytral pits not impressed and weakly outlined. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

*Integument sculpture.* Punctures 30 microns in diameter dorsally, but 15 to 20 microns in diameter on elytral intervals 4, 6 and 8, and 40 microns in diameter ventrally. Punctures 15 to 30 microns apart dorsally except antero-laterally on pronotum (30 to 40 microns apart) and in elytral pits (10 to 20 microns apart).

Microsculpture convex on dorsal and ventral surfaces, but flat on abdominal sterna.

*Male genitalia.* Apex of median lobe in ventral view, thin-edged and straight (Fig. 55b), and in lateral view moderately long, round and wide (Fig. 55c). Setae of parameres long (Fig. 53c).

*Measurements and proportions.*— Three samples studied, data for two presented in Tables 41 and 42.

*Variation.*— Samples from Austria, Yugoslavia and Caucasus are very similar, but the mean of ratios PL/EL and PW/EL is significantly smaller for the Caucasus sample than for those of middle Europe. Thus, there is evidence that *E. tschitscherini* may represent a geographical race. However, larger samples are needed to clarify this problem.

#### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of subsequently described species by short epicranial suture (0.25 as long as antennomere 1), and restricted microsculpture on parietale (2% of latero-ventral surface).

*Description.*— Parietale dark brown dorsally but paler behind eyes and along base; nota and terga dark brown. Apical inner margin of mandible and posterior margin of retinaculum clearly toothed; retinaculum narrow (about 2.5

times wider than long). Setae MP and EM-P of frontale lacking, though puncture present. Epicranial suture 0.25 as long as antennomere 1. Parietale with microsculpture laterally (10% of latero-dorsal and 2% of latero-ventral surface), and without pointed microsculpture; mesonotum and metanotum without pointed microsculpture near suture. Microsculpture of terga single-pointed.

## Second and Third Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by short epicranial suture (0.25 length of antennomere 1), and lack of microsculpture laterally on parietale.

## Second Instar Larvae

*Description.*— Nota and terga dark brown. Parietale without microsculpture laterally, and pointed microsculpture. Each sclerite of pronotum with less than 30 accessory setae, and without microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A medium-sized; each sclerite with less than 20 accessory setae, and lateral band with one or two accessory setae; pointed microsculpture present laterally (15% of surface). Largest projection on urogomphus small in lateral view: 0.5 as long as width of urogomphus below. Each sclerite of terga 1 to 8 with about 15 accessory setae. Urogomphus without very small accessory setae. Base of tergum 10 with fine multi-pointed microsculpture. Abdominal epipleura 2 to 7 with five to seven accessory setae; microsculpture single-pointed. Abdominal hypopleura 2 to 7 with three to five accessory setae and some large. Membrane microsculpture consisting of fine points.

## Third Instar Larvae

*Description.*— Parietale with microsculpture restricted dorso-laterally (less than 5% of surface), and without pointed microsculpture. Each sclerite of pronotum with about 30 accessory setae. Mesonotum and metanotum with pointed sculpture on lateral portions only (10% surface). Lateral band of terga 1 to 8 narrow, not enlarged posteriorly, and with less than 12 accessory seta; terga with about 30 accessory setae on each sclerite. Abdominal epipleuron 1 with eight to ten accessory setae, and epipleura 2 to 7 with about 20. Abdominal hypopleura 2 to 7 with about 15 accessory setae.

## Geographical Distribution and Affinities, and Notes

*Distribution.*— This is a middle European species ranging from Germany and Poland in the North, to France, the Northern shore of the Mediterranean, and Bulgaria in the South, but isolated in the Caucasus (Turin *et al.*, 1977). I have seen specimens from France, Germany, Poland, Yugoslavia, Czechoslovakia, Bulgaria, Austria and the Caucasus.

*Taxonomic notes.*— I have not seen Dejean's type of *E. littoralis*, but the description leaves no doubt as to the identity of his specimen with this species. The description of *E. smaragdinus* matches that of *E. aureus* except for greener surface (Semenov, 1907). Semenov (1897, 1926) recognized *E. tschitscherini* because of the isolated distribution of his type series relative to that of *E. aureus* and *E. angusticollis longicollis*. I have seen eight specimens from the Caucasus, and they match almost perfectly those of *E. aureus*. The Caucasus population may be a glacial relic.

I studied about 120 adults and dissected six males. I examined three first instar, two second instar and four third instar larvae from Austria.

*Collecting notes.*— Bauer (1976) collected adults on moist and bare soil along margins of rivers with moderate current near the forest zone. He did not specify if adults run on sun-exposed or shaded surfaces. However, adults of this and following species are found on upper beaches away from water.

*Geographical affinities.*— The ranges of this species and *E. ulrichi* overlap.

### *Elaphrus purpurans* Hausen

Figs. 27, 56a-c, 74, 86, 92a-b, 102a-b, 173

*Elaphrus pallipes* Horn, 1878:51. Type area: Oregon and British Columbia; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. Junior homonym of *E. pallipes* Duftschmid 1812:197. (= *Asaphidion*



Table 43. Descriptive statistics for *E. purpurans*, based on ten males and ten females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.40–1.60	1.50	0.077	0.023	3.4
PW	1.49–1.60	1.53	0.080	0.024	3.5
EL	3.60–4.25	3.96	0.271	0.081	4.5
EW	1.32–1.52	1.45	0.078	0.023	3.6
HW	1.70–1.90	1.81	0.100	0.030	3.7
B. Proportions					
PL/PW	0.937–1.000	0.975	0.031	0.010	2.2
PL/EL	0.360–0.393	0.379	0.013	0.004	2.4
PL/EW	0.983–1.069	1.030	0.028	0.008	1.8
PL/HW	0.776–0.853	0.828	0.028	0.008	2.3
PW/EL	0.372–0.410	0.388	0.015	0.004	2.6
PW/EW	1.033–1.113	1.057	0.030	0.008	1.9
PW/HW	0.817–0.875	0.849	0.027	0.008	2.1
EL/EW	2.632–2.833	2.722	0.085	0.026	2.1
EL/HW	2.055–2.297	2.187	0.082	0.024	2.5
EW/HW	0.779–0.833	0.804	0.024	0.008	2.0

*pallipes* Duftschmid), discovered by Silverberg (1977). Schaupp, 1878:6. Austin, 1880:5. Wickham, 1893:202, 203. Keen, 1905:297. Van Dyke, 1924:3. Clark, 1948:25. Hatch, 1953:63. Lindroth 1961:119.

*Elaphrus purpurans* Hausen, 1891:251. Type area: British Columbia; type not seen. Hatch, 1953:11. Lindroth, 1961:119.

## Adults

**Diagnostic combination.**— Distinguished from adults of other species by unbeaded lateral margin of pronotum, by presence of two distinct metallic green spots on dorsum of femur, and by projection at base of posterior spur of tibia of foreleg (much larger in males than in females).

**Description.**— Three distinct color forms. Gray-green form: microsculptured surface dark copper and punctures green or blue-green--areas with dense puncture gray-green and those with scattered punctures dark copper. Copper form: head and pronotum with punctures and microsculptured surfaces bright copper; elytra bright copper at base and along outer 0.5, remainder as in gray-green form. Dark form (absent east of Rockies): head, pronotum, inner 0.5 and apical 0.3 of elytra as in gray-green form; base and outer 0.5 of elytra with purple or dark blue punctures and microsculptured areas. Elytral pits purple near setigerous puncture. Femora with two metallic spots on dorsum.

Antennomere 4 pubescent in apical 0.5. Pronotum with lateral margin unbeaded with setigerous puncture near hind angle of pronotum, and with one pair of weakly outlined submedial impressions. Prosternal process without accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal sterna 4, 5 and 6 with 18 to 25 accessory setae. Elytral mirrors in two to three rows, sharply outlined, and slightly convex; sutural mirrors with first, or first and third mirrors wider. Elytral pits weakly outlined and not impressed. Secondary sexual characters of males typical of genus, but without projection at base of inner spur of tibia of midleg. Trochanter of midleg with one seta. Tibia of foreleg with projection present at base of posterior spur (much larger in males than in females).

**Integument sculpture.** Punctures 20 to 25 microns in diameter on elytron and head, 25 microns in diameter on pronotum, and 25 to 30 microns in diameter on ventral surface. Punctures 5 to 15 microns apart dorsally, but 5 microns apart in pits, and 50 to 70 microns apart antero-laterally on pronotum.

Table 44. Descriptive statistics for *E. purpurans*, based on nine males and 11 females from McMinnville, Oregon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.50	0.085	0.025	3.8
PW	1.40–1.60	1.49	0.082	0.024	3.6
EL	3.40–3.90	3.67	0.201	0.060	3.6
EW	1.25–1.45	1.34	0.082	0.024	4.1
HW	1.72–1.92	1.81	0.079	0.024	2.9
B. Proportions					
PL/PW	0.950–1.071	1.011	0.048	0.014	3.2
PL/EL	0.387–0.446	0.412	0.021	0.006	3.4
PL/EW	1.071–1.200	1.122	0.048	0.016	3.2
PL/HW	0.792–0.870	0.835	0.031	0.010	2.5
PW/EL	0.390–0.432	0.407	0.015	0.004	2.5
PW/EW	1.071–1.154	1.110	0.033	0.010	2.0
PW/HW	0.800–0.863	0.826	0.025	0.008	3.1
EL/EW	2.643–2.808	2.727	0.059	0.018	1.4
EL/HW	1.943–2.113	2.029	0.074	0.022	2.4
EW/HW	0.714–0.768	0.744	0.028	0.008	2.6

Microsculpture of dorsal and ventral surfaces subconvex to convex, but subconvex to flat on abdominal sterna.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 56c), and in lateral view extremely wide and subtruncate (Fig. 56a). Setae of paramere short (Fig. 56b).

*Measurements and proportions.*— Six samples studied, and data for two presented in Tables 43 and 44.

*Variation.*— Samples across the range are rather similar. However, west of the Rockies, three color forms occur while only two are known to the east (dark form lacking). Also the largest projection of urogomphus of the second and third instar larvae is smaller east of the Rockies than west of them (based on one sample from coastal Oregon and a few samples from Alberta).

The variation between samples is clinal from Alberta and Alaska to California as shown by ratios PL/EW, PW/EL, EL/HW and EW/HW. However, two groups are suggested: one including samples from Alberta, Alaska and coastal Washington, and another including samples from south central British Columbia, Oregon and California. The northern group have significantly smaller means for ratio PL/EL, and larger means for ratio PW/HW than those of the southern group.

Because of limited number of samples, the data are not sufficient for conclusions. This preliminary information may be useful in future studies of infraspecific variation in this species.

#### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of *E. aureus* by long epicranial suture, by smooth apical inner margin of mandible and posterior margin of retinaculum, and by

presence of pointed microsculpture dorso-laterally on parietale. Distinguished from subsequently described species by lack of setae MP and EM-P on frontale, and by restricted microsculpture latero-ventrally on parietale (5% of surface).

**Description.**—Parietale brown dorsally but paler behind eyes and base; nota and terga brown. Apical inner margin of mandible and posterior margin of retinaculum barely toothed or smooth; retinaculum normal (about 2 times wider than long). Setae MP and EM-P of frontale lacking, though punctures present. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Parietale with microsculpture laterally (30% of dorsal and 5% of ventral surface), and without pointed microsculpture dorsally (5% of surface). Mesonotum (at base) and metanotum with pointed sculpture near suture. Microsculpture of abdominal terga single-pointed.

### Second and third Instar Larvae

**Diagnostic combination.**—Distinguished from larvae of *E. aureus* by long epicranial suture, and by presence of some pointed sculpture laterally on parietale. Distinguished from subsequently described species by lack of very small accessory setae on urogomphus surface.

### Second Instar Larvae

**Description.**—Nota and terga brown. Parietale with microsculpture restricted laterally (5% of ventral and dorsal surfaces), and with pointed microsculpture restricted laterally (3% of dorsal and 5% of ventral surfaces). Each sclerite of pronotum with about 35 accessory setae, and without microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A medium-sized; each sclerite with about 40 accessory setae, and lateral band with one or two accessory setae; pointed microsculpture widespread laterally (30% of disc surface) and at base near suture. Largest projection of urogomphus short in lateral view (0.3 to 0.5 as long as width of urogomphus below). Each sclerite of terga 1 to 8 with about 15 accessory setae. Urogomphus without very small accessory setae. Base of tergum 10 with fine multipointed microsculpture. Abdominal epipleura 2 to 7 with five to seven accessory setae; pointed microsculpture single-pointed. Abdominal hypopleura 2 to 7 with three to five accessory setae and some large. Membrane microsculpture consisting of fine points.

### Third Instar Larvae

**Description.**—Parietale with microsculpture laterally (20% of dorsal and 5% of ventral surface), and with restricted pointed microsculpture laterally (5% of ventral surface). Each sclerite of pronotum with about 45 accessory setae. Mesonotum and metanotum with pointed microsculpture on lateral portion only (10 to 15% of surface). Lateral band of terga 1 to 8 narrow (not enlarged posteriorly) and with less than 12 accessory setae; terga 1 to 8 with about 35 accessory setae on each sclerite. Abdominal epipleuron 1 with eight to ten accessory setae, and epipleura 2 to 7 with about 20. Abdominal hypopleura 2 to 7 with about 15 accessory setae.

### Geographical Distribution and Affinities, and Notes

**Distribution.**—A western Nearctic species extending from forested regions of the Pacific coast (between Alaska and central California) east to Mackenzie River, Northwest Territories, Alberta, Idaho, and western Oregon and California (Fig. 173).

**Taxonomic notes.**—I have not seen the type of *E. purpurans* but the description clearly refers to the copper form of this species where, in British Columbia, (the type area), there is no other copper colored *Elaphroterus*.

I studied about 1000 adults and dissected nine males. I examined six first instar, four second instar and three third instar larvae from Conjuring Creek, Alberta, and three third instar larvae from western Oregon.

**Collecting notes.**—Adults are less hygrophilous, run in the shade, and are found on upper beaches of rivers. The surface is bare or covered with leaf litter. The soil consists of sand, silt, or a mixture of both. The slope of the beaches varies from flat to almost vertical. Adults are found along rivers originating from mountains with summer melting period or for a few kilometers along adjoining creeks. I found adults along torrential glacial rivers where water levels may fluctuate as much as three meters a day, and along slow and warm creeks (Conjuring Creek,

Alberta) with moderate and irregular water level fluctuations. The life cycle is typical of the genus as outlined under *E. clairvillei*. I found only one larva on an upper beach. I do not know where adults overwinter.

*Geographical affinities.*— Sympatric with *E. angusticollis angusticollis* in subarctic regions.

### *Elaphrus angusticollis* Sahlberg

#### Adults

*Diagnostic combination.*— Distinguished from adults of preceeding species by traceable but unbeaded lateral margin of pronotum, and from those of *E. ulrichi* by presence of setigerous puncture near hind angle of pronotum. Most similar to adults of *E. purpurans*, but separated on femora color: dark brown below and dark metallic green above (metallic spot not divided in two).

*Variation.*— Under this name, two distinct forms are recognized: one extending from northern Europe east to the Yenisey River, and another from the Lena River, in eastern Siberia, to the Pacific coast, and from Alaska east to the Mackenzie River. Adults of each form are distinguished by characters, described below, under each subspecies.

Similar groupings are clearly suggested following comparisons of means of many ratios between three samples. The ratio EL/HW between adults of *E. angusticollis angusticollis* and *E. angusticollis longicollis* is significantly and taxonomically different. Also samples of *E. angusticollis angusticollis* relative to those of the other subspecies show significantly larger means for ratios PW/EW, EL/EW and EW/HW, and smaller means for ratios PL/EL, PL/EW and PW/EL.

Because of marked differences in many structural and in one behavioural characters, the lack of clinal variation, and the allopatric distribution of these two forms, I feel they should be considered at least subspecifically distinct.

### *Elaphrus angusticollis angusticollis* Sahlberg

Figs. 26, 58, 113, 125, 151, 152, 156, 173

*Elaphrus angusticollis* R.F. Sahlberg, 1844:20. Type locality: Ochota River near Ochotsk (eastern Siberia), USSR; type not seen. Sahlberg, 1880:11. Marseul, 1882:4. Semenov, 1904c:105. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

*Elaphrus angustatus* Chaudoir, 1850:161. Type area: Eastern Siberia; type not seen. Sahlberg, 1880:11. Marseul, 1882:4. Semenov, 1895:306. 1904c:104. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

#### Adults

*Diagnostic combination.*— Distinguished from adults of *E. angusticollis longicollis* as follows: elytral mirrors convex; punctures on elytral intervals 4, 6 and 8 denser (10 to 20 microns apart); many accessory setae on hind coxa (10 to 20), on side of metasternum (abundant), and on abdominal sterna 4, 5 and 6 (10 to 20).

*Description.*— Three color forms. Gray-green form: microsculptured surface dark copper and punctures green or blue-green dorsally; mouthparts and antennomere 1, 2 and 3 bright copper; femur golden or bright copper. Green form: microsculptured surface copper (usually brighter than gray-green form) and punctures green or blue-green dorsally; mouthparts, antennomere 1, 2 and 3, and femora bright green. Copper form: head, pronotum, base and outer 0.5 of elytra with bright copper microsculptured surfaces and punctures; inner 0.5 and apex of elytra as in gray-green form. Femora of all forms metallic on dorsum and not divided.

Antennomere 4 pubescent in apical 0.5. Pronotum with lateral margin unbeaded but traceable except in sinuation, with setigerous puncture near hind angle of pronotum, and with one pair of weakly outlined submedial impressions. Prosternal process without accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal

Table 45. Descriptive statistics for *E. angusticollis angusticollis*, based on ten males and ten females from Omsukschan, USSR (eastern Siberia).

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.40–1.57	1.48	0.082	0.024	3.7
PW	1.45–1.70	1.57	0.084	0.025	3.6
EL	3.90–4.40	4.15	0.218	0.065	3.5
EW	1.40–1.62	1.50	0.088	0.026	3.9
HW	1.70–1.90	1.79	0.076	0.023	2.8
<b>B. Proportions</b>					
PL/PW	0.882–0.984	0.939	0.045	0.014	3.2
PL/EL	0.341–0.367	0.356	0.012	0.004	2.0
PL/EW	0.923–1.034	0.986	0.045	0.014	3.0
PL/HW	0.781–0.863	0.824	0.034	0.010	2.8
PW/EL	0.366–0.400	0.379	0.017	0.006	2.9
PW/EW	0.985–1.086	1.050	0.043	0.012	2.8
PW/HW	0.833–0.944	0.877	0.033	0.010	2.5
EL/EW	2.667–2.900	2.772	0.094	0.028	2.3
EL/HW	2.192–2.411	2.317	0.095	0.028	2.7
EW/HW	0.789–0.890	0.836	0.042	0.012	3.3

sterna 4, 5 and 6 with 10 to 20 accessory setae. Elytral mirrors in three rows, sharply outlined, and convex; first, or first and third sutural mirrors wider. Elytral pits weakly impressed and outlined. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

*Integument sculpture.* Punctures 20 to 25 microns in diameter dorsally. Punctures 10 to 20 microns apart dorsally, but 5 to 10 microns apart in pits and 40 to 50 microns apart antero-laterally on pronotum.

Microsculpture convex dorsally, and convex or subconvex on ventral surface.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 57a), and in lateral view quite wide and round (Fig. 58). Setae of paramere short (Fig. 56b).

*Measurements and proportions.*— Two samples studied, data for one presented in Table 45.

*Variation.*— Adults from Inuvik, Northwest Territories are most similar to those from eastern Siberia. Both samples show three color forms in similar proportion. I found no evidence of clinal variation in any characters.

### All Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by paler parietale: dark brown only near frontale and epicranial suture.

### First Instar Larvae

*Description.*— Parietale pale except near frontale and epicranial suture; nota and terga dark brown. Apical inner margin of mandible and posterior margin of retinaculum smooth; retinaculum normal (about twice as wide as long). Seta MP and EM-P of frontale very small. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Parietale with widespread microsculpture laterally (80% of dorsal and 30% of ventral surfaces), and with widespread pointed microsculpture laterally (50% of dorsal and 20% of ventral surfaces). Mesonotum and metanotum with pointed sculpture near suture. Sculpture of abdominal terga single-pointed.

## Second Instar Larvae

**Description.**— Nota and terga dark brown. Parietale with widespread microsculpture laterally (30% of dorsal and 15% of ventral surfaces), and with restricted pointed microsculpture laterally (5% of dorsal and 15% of ventral surfaces). Each sclerite of pronotum with about 45 accessory setae, and with pointed microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A small; each sclerite with about 40 accessory setae and lateral band with one to five accessory setae; pointed microsculpture widespread laterally (20% of surface) and moderately widespread near suture (10% of surface). Largest projection of urogomphus small in lateral view: 0.5 as long as width of urogomphus below. Each sclerite of terga 1 to 8 with about 30 accessory setae. Urogomphus with numerous very small accessory setae. Base of tergum 10 with coarse multi-pointed microsculpture. Abdominal epipleura 2 to 7 with 10 to 15 accessory setae; microsculpture multi-pointed. Abdominal hypopleura 2 to 7 with six to eight accessory setae, and largest ones small. Membrane microsculpture coarse.

## Third Instar Larvae

**Description.**— Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with restricted pointed microsculpture latero-ventrally (5% of disc surface). Each sclerite of pronotum with about 60 accessory setae. Each sclerite of mesonotum and metanotum with more than 50 accessory setae, with widespread pointed microsculpture laterally (20 to 25% of surface) and without pointed microsculpture near suture. Lateral band of terga 1 to 8 narrow, not enlarged posteriorly, with about 12 accessory setae; terga 1 to 8 with about 45 accessory setae on each sclerite. Abdominal epipleuron 1 with 10 to 12 accessory setae, and epipleura 2 to 7 with about 25. Abdominal hypopleura 2 to 7 with about 20 accessory setae.

## Geographical Distribution and Affinities, and Notes

**Distribution.**— This subarctic subspecies ranges from the Lena River in eastern Siberia to the Bering Sea, and from Alaska to the MacKenzie Delta, Northwest Territories. The North American distribution is illustrated in Fig. 173.

**Taxonomic notes.**— I have seen one seemingly original Sahlberg specimen. It matches adults of this subspecies. I have not seen the type of *E. angustatus*, but it came from a locality inside the range of this subspecies.

I have studied about 250 adults and dissected six males. I examined four first instar, four second instar and six third instar larvae from Inuvik, Northwest Territories.

**Collecting notes.**— Adults are less hygrophilous, are found on upper beaches, and run in sunny locations on bare soil with sparse *Equisetum fluviatile* Linnaeus, or on soil with some leaf litter in the willow zone. At Inuvik, Northwest Territories, adults were found only near the MacKenzie River on silty banks. Adults of this subspecies seem restricted to large subarctic rivers. Lindroth (1961) observed that wings are variable in length, and may not be functional.

**Geographical affinities.**— The range of this subspecies overlaps only that of *E. purpurans*.

### *Elaphrus angusticollis longicollis* Sahlberg

Fig. 57a-b

*Elaphrus longicollis* J. Sahlberg, 1880:11. Type locality: Turuchansk on Yenisey River (western Siberia) subsequently designated by Lindroth (1961); lectotype, female from the same locality designated by Lindroth and deposited at the Swedish Riksmuseum, Stockholm. Semenov, 1895:307. 1904c:104. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

*Elaphrus jakovlewi* Semenov, 1895:303. Type locality: Jamburg near Leningrad, USSR; type not seen. Semenov, 1897:596. 1904c:104. Lindroth, 1961:120.

*Elaphrus jakovlewi* ab. *costulatus* Semenov, 1895:305. Semenov does not suggest a type locality or type specimen.

*Elaphrus jakovlewi*; Lindroth, 1939:66. Palmén, 1944:24. Invalid emendation.

## Adults

**Diagnostic combination.**— Distinguished from adults of *E. angusticollis angusticollis* as follows: elytral mirror flat; punctures sparse on elytral intervals 4, 6 and 8 (30 to 40 microns

Table 46. Descriptive statistics for *E. angusticollis longicollis*, based on ten males and ten females from USSR (Salmi, Suomi, Metsäpertti).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.67	1.56	0.106	0.032	4.5
PW	1.45–1.72	1.59	0.124	0.037	5.2
EL	3.50–4.25	3.84	0.288	0.085	3.9
EW	1.30–1.62	1.45	0.123	0.037	5.7
HW	1.72–2.02	1.86	0.115	0.034	4.1
B. Proportions					
PL/PW	0.913–1.031	0.979	0.045	0.014	3.1
PL/EL	0.375–0.434	0.407	0.018	0.006	2.9
PL/EW	1.017–1.143	1.078	0.049	0.014	3.1
PL/HW	0.800–0.877	0.836	0.036	0.010	2.9
PW/EL	0.375–0.433	0.416	0.019	0.006	3.1
PW/EW	1.017–1.140	1.101	0.043	0.012	2.6
PW/HW	0.811–0.901	0.854	0.033	0.010	2.6
EL/EW	2.571–2.731	2.648	0.070	0.022	1.8
EL/HW	1.973–2.162	2.054	0.072	0.022	2.3
EW/HW	0.732–0.803	0.776	0.031	0.010	2.7

apart); few accessory setae on hind coxa (two to five), lacking laterally on metasternum, and on abdominal sterna 4, 5 and 6 (one to eight).

**Description.**— One color form – dark blue-gray: microsculptured surfaces forming mosaic of dark copper, purple and black surfaces dorsally; punctures green or blue-green.

Abdominal sterna 4, 5 and 6 with one to eight accessory setae. Elytral mirrors in three rows and flat. Elytral pits not impressed and slightly outlined.

**Integument sculpture.** Punctures 15 to 20 microns in diameter dorsally. Punctures 30 to 40 microns apart on intervals 4, 6 and 8, 10 to 20 microns apart in pits, and 50 to 70 microns apart antero-laterally on pronotum.

**Male genitalia.** Apex angular, otherwise as that of *E. angusticollis angusticollis* (Fig. 57b).

**Measurements and proportion.**— One sample studied. See Table 46.

**Variation.**— Specimens from the Baltic sea and the Yenisey River are similar. There is no evidence of clinal variation in any characters.

**Distribution.**— A Palaearctic subspecies known in subarctic region from the Baltic Sea to Yenisey River.

**Taxonomic notes.**— I have seen adults of this subspecies from the type locality of *E. jakovlewi* and from Dudinka near type locality of *E. longicollis*. Therefore both names are probably synonymous.

I have examined about 40 adults and dissected five males.

**Collecting notes.**— Habitat similar to that of *E. angusticollis angusticollis*, but adults are found in the shade of taller vegetation (Palmén and Platonoff, 1943).

**Geographical affinities.**— The range does not overlap that of other species.

Table 47. Descriptive statistics for *E. ulrichi*, based on ten males and ten females from Carinthia, Austria.

Character	Range	Mean	1.5SD	2SE	CV(%)
<b>A. Measurements in mm.</b>					
PL	1.35–1.90	1.73	0.166	0.050	6.4
PW	1.37–1.90	1.78	0.180	0.054	6.7
EL	4.05–4.85	4.44	0.257	0.077	3.8
EW	1.42–1.67	1.58	0.096	0.029	4.0
HW	1.70–2.22	2.08	0.169	0.050	5.4
<b>B. Proportions</b>					
PL/PW	0.932–1.015	0.970	0.033	0.010	2.3
PL/EL	0.293–0.422	0.390	0.039	0.012	6.7
PL/EW	0.806–1.169	1.094	0.112	0.034	6.8
PL/HW	0.614–1.059	0.833	0.113	0.034	9.1
PW/EL	0.299–0.432	0.402	0.040	0.012	6.7
PW/EW	0.821–1.206	1.127	0.118	0.036	7.0
PW/HW	0.625–1.088	0.858	0.117	0.036	9.1
EL/EW	2.656–3.018	2.803	0.124	0.038	3.0
EL/HW	1.952–2.676	2.134	0.208	0.062	6.5
EW/HW	0.695–0.971	0.762	0.079	0.034	6.9

*Elaphrus ulrichi* Redtenbacher

Figs. 59a-b, 103a-b

*Elaphrus ulrichi* Redtenbacher, 1842:5. Type area: Austria: type not seen. Letzner, 1849:52. Schaum, 1856:73. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Fauvel, 1882:82, 83. Marseul, 1882:4. Reitter, 1887:17. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:306, 317. Jacobson, 1096:268. Reitter, 1908:96, 97. 1909:106. Kuhn, 1912:50. Schaufuss, 1916:29. Porta, 1923:78.

*Elaphrus ulrichii* Gaubil, 1849:14 (invalid emendation).

*Elaphrus smaragdinus* Knorlein (In: Schaum, 1856:73). NOMEN NUDUM.

*Elaphrus austriacus* Ulrick (In: Schaum, 1856:73). NOMEN NUDUM. Semenov, 1895:317.

*Elaphrus beraneki* Reitter, 1887:242. Type area: Czechoslovakia in Tabor, Bohemia; type not seen. Ganglbauer, 1892:123, 124. Jacobson, 1906:268.

*Elaphrus baraneki* Semenov, 1895:317 (invalid emendation).

*Elaphrus ullrichi* Semenov, 1895:317 (invalid emendation).

**Adults**

**Diagnostic combination.**— Distinguished from adults of other species by lack of setigerous puncture near hind angle of pronotum, and by lack of accessory setae along posterior area of metasternum.

**Description.**— Dorsal surface emerald green with numerous copper reflecting surfaces. Microsculptured areas copper (darker on elytral intervals and brighter on pronotum) and green. Punctures green or blue-green, but purple in elytral pits. Elytra appearing brighter green laterally resulting from nearly black microsculptured surfaces with green punctures. Elytral pits sharply outlined against dark copper intervals. Femora red-brown with dorsal side bright green.

Antennomere 4 with few apical setae mostly on posterior side. Pronotum with lateral margin unbeaded but traceable, without setigerous puncture on hind angle, and without medial impression. Prosternal process without accessory setae. Metasternum with few accessory setae antero-medially, and without setae posteriorly. Abdominal sterna 4, 5 and 6 with



less than 4 accessory setae. Elytral mirrors in one or two rows, clearly outlined and flat; first, or first and third sutural mirrors wider. Elytral pits slightly impressed and sharply outlined against darker intervals. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

*Integument sculpture.* Punctures 15 to 20 microns in diameter on elytra and head, 25 to 30 microns in diameter on pronotum and ventral surfaces. Punctures 5 to 10 microns apart on elytra, and 10 to 20 microns apart medially and 50 to 100 microns apart laterally on pronotum.

Microsculpture subconvex on green, blue-green and purple surfaces and flat on or absent from copper and ventral surfaces.

*Male genitalia.* Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 59a) and in lateral view very wide with ventral bulge (Fig. 59b). Setae of parameres long (Fig. 56b).

*Measurements and proportions.*— I studied one sample, see Table 47.

*Variation.*— I observed no evidence of geographical variation.

### First Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by red-brown anterior portion of pronotum and tergum 1 (Bauer 1976), and by multipointed microsculpture on abdominal terga.

*Description.*— Anterior portion of pronotum and tergum 1 red-brown; except for pale areas at base of parietale and behind eyes, head, nota and terga dark brown (Bauer, 1976). Apical inner margin of mandible and posterior margin of retinaculum smooth; retinaculum normal (about twice as wide as long). Seta MP and EM-P on frontale very small. Epicranial suture 0.4 to 0.5 length of antennomere 1. Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with widespread pointed microsculpture laterally (20% of dorsal and 10% of ventral surfaces). Mesonotum and metanotum without pointed sculpture. Microsculpture on abdominal terga multipointed.

### Second and Third Instar Larvae

*Diagnostic combination.*— Distinguished from larvae of other species by unusual dorsal coloration: pronotum, tergum 1 and lateral 0.3 of terga 2 to 7 reddish-brown, rest dark brown.

#### Second Instar Larvae

*Description.*— Pronotum, tergum 1 and external 0.3 of terga 2 to 7 red-brown, mesonotum, metanotum, inner 0.7 of terga 2 to 7, and tergum 9 dark brown.

Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with moderately widespread pointed microsculpture (5% of dorsal and 15% of ventral surfaces). Each sclerite of pronotum with about 45 accessory setae, and with pointed microsculpture on lateral band. Mesonotum and metanotum with setae PIE-A small; each sclerite with about 40 accessory setae, and lateral band with one to five accessory setae; pointed sculpture widespread laterally (20% of surface), moderately widespread near suture (10% of surface). Largest projection of urogomphus in lateral view absent or barely apparent (Fig. 103a). Each sclerite of terga 1 to 8 with about 30 accessory setae. Urogomphus with numerous very small accessory setae. Base of tergum 10 with scale-like and meshed microsculpture. Abdominal epipleura 2 to 7 with more than 15 accessory setae; microsculpture multi-pointed. Abdominal hypopleura 2 to 7 with eight or more small accessory setae. Membrane with barely suggested pointed microsculpture at high magnification (250 X).

#### Third Instar Larvae

*Description.*— Parietale with widespread microsculpture laterally (60% of dorsal and 15% of ventral surfaces), and without pointed microsculpture. Each sclerite of pronotum with about 60 accessory setae. Mesonotum and metanotum with pointed microsculpture restricted laterally (5% of surface), and absent near suture. Terga 1 to 8 with lateral band enlarged (wider posteriorly), and with more than 15 accessory setae. Abdominal epipleuron 1 with four accessory setae, and epipleura 2 to 7 each with about 40. Abdominal hypopleura 2 to 7 each with about 20 accessory setae.

### Geographical Distribution and Affinities, and Notes

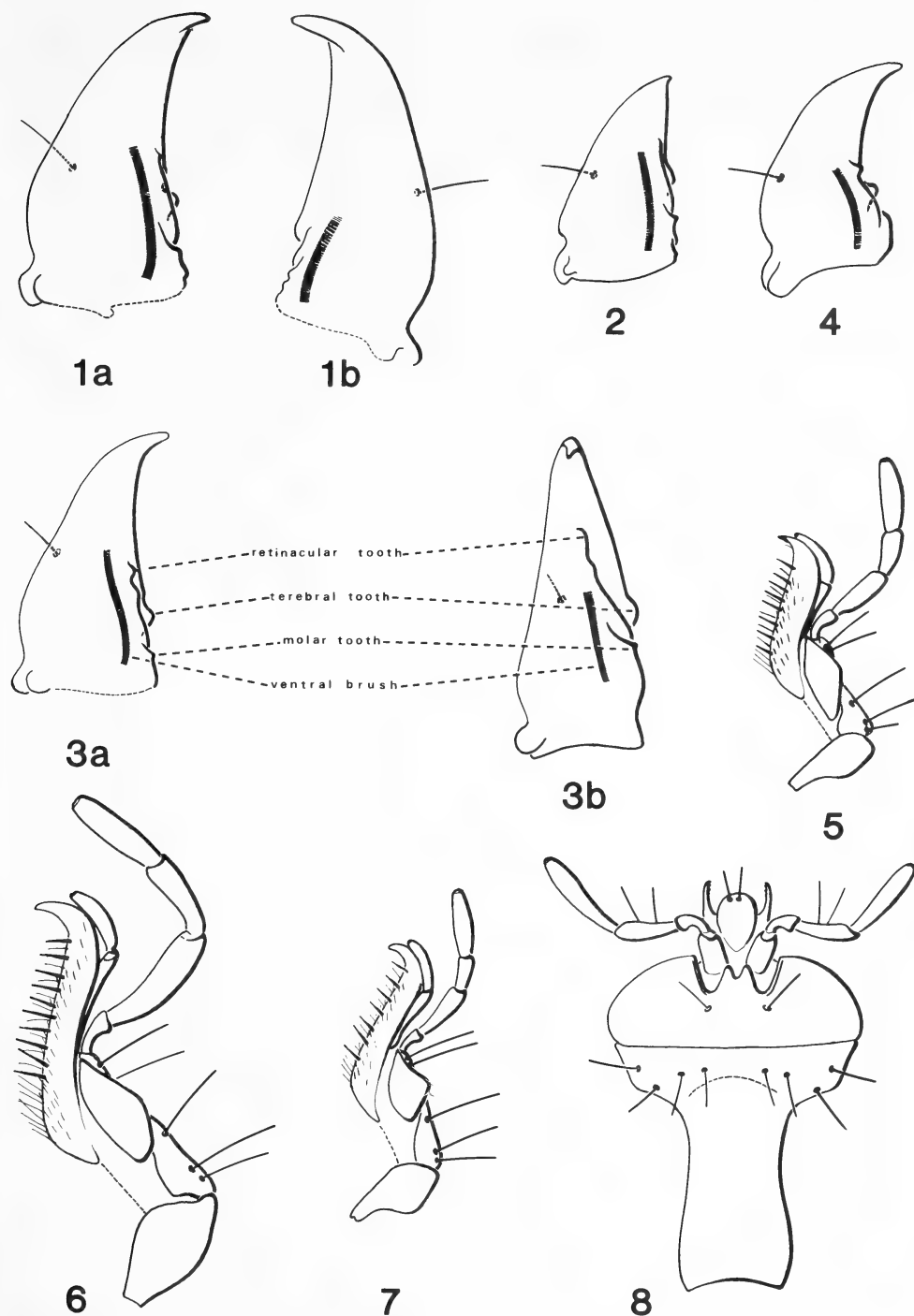
*Distribution.*— A middle European species recorded from The Netherlands, eastern France, northern Italy, Switzerland, Austria, Germany, Poland, Hungary and Czechoslovakia (Turin, *et al.*, 1977). I have not seen specimens from Italy, Poland, Hungary and The Netherlands.

*Taxonomic notes.*— *E. ulrichi* is easily distinguished from the original description. According to the description of *E. beraneki*, the type is apparently a dark color variant.

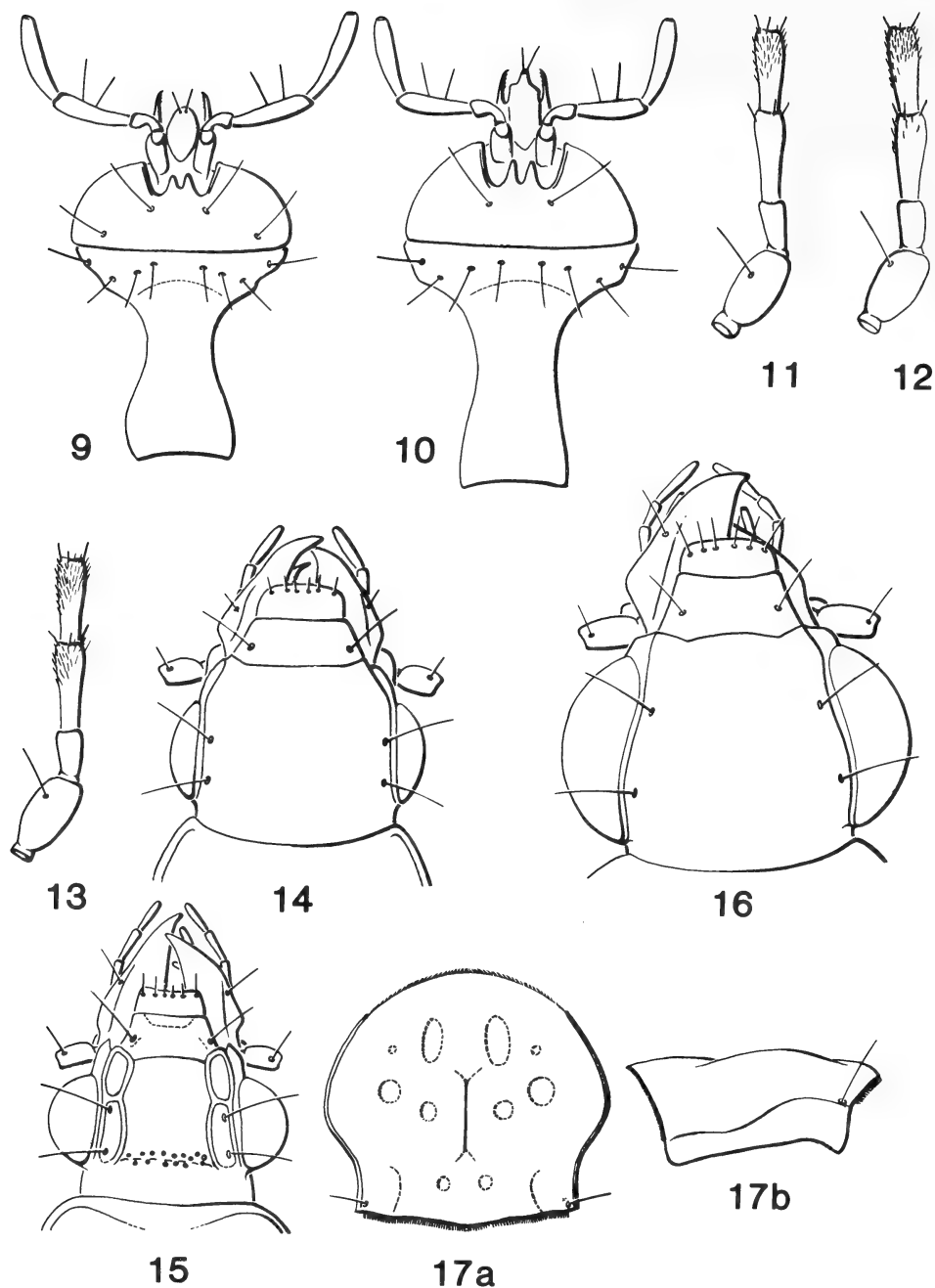
I studied about 60 adults and dissected three males. I examined three first instar, one second and one third instar larvae from Austria.

*Collecting notes.*— Adults of this species are found away from water on firm sandy overflows with scattered vegetation along mountain rivers with moderate current (Bauer, 1976). Bauer (1976) observed that larvae, especially of the second and third instar, match the color pattern of adults of poisonous staphylinids *Paederus ruficollis* Fabricius. Smetana (1949) collected adults of *E. ulrichi* in a similar habitat in Czechoslovakia, along with adults of *P. ruficollis* and those of a larger species *P. rubrothoracicus* Goeze. Adults of *P. ruficollis* are similar in size to second instar larvae of *E. ulrichi*, and of *P. rubrothoracicus* and to third instar larvae of *E. ulrichi*. Bauer (1976) showed that *P. ruficollis* is strongly avoided by *Actitis hypoleucos* (Linnaeus), a common species of bird in this habitat. Thus, he suggested that the larval colors are possibly the result of mimicry.

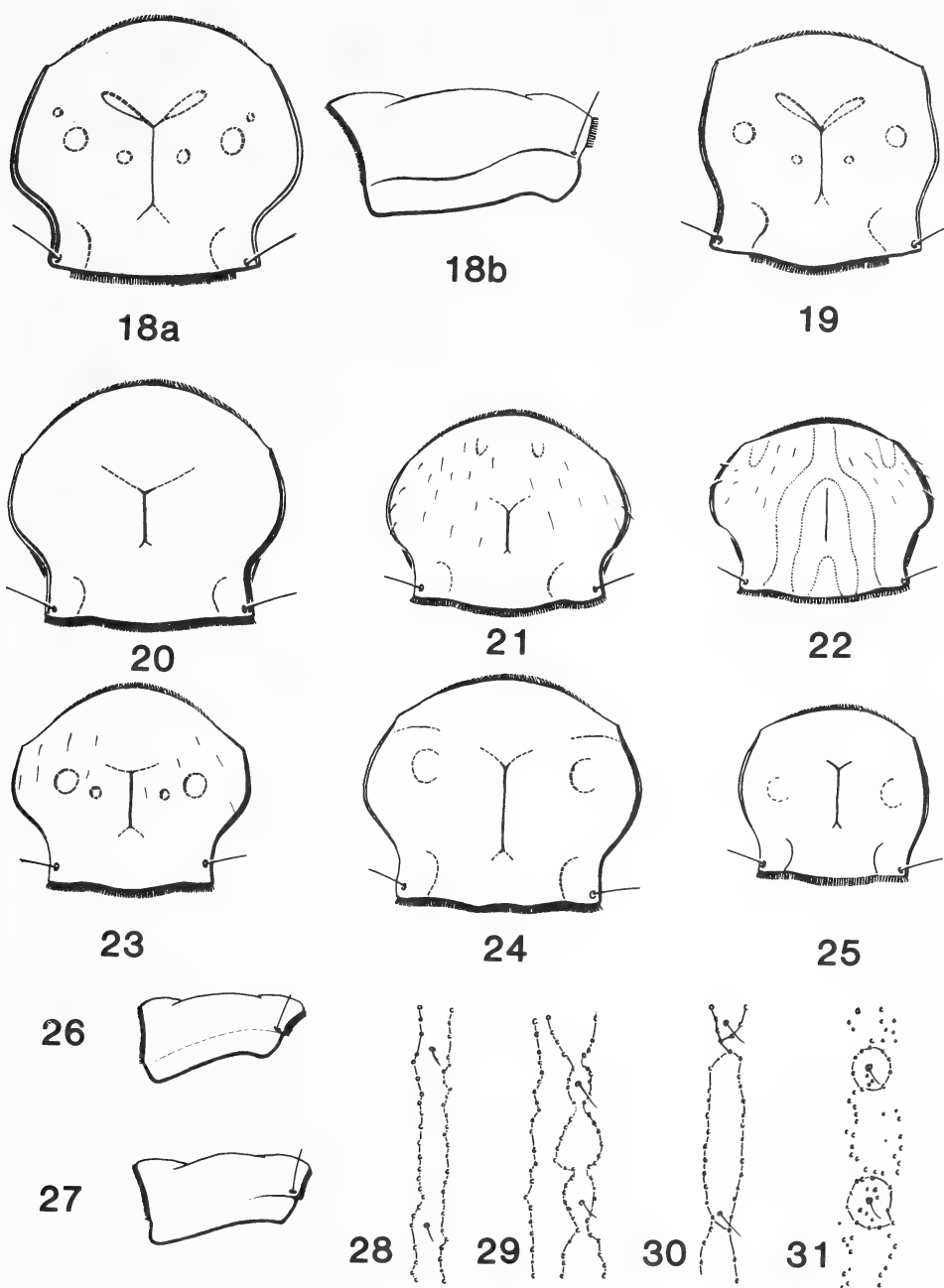
*Geographical affinities.*— The ranges of this species and *E. aureus* overlap.



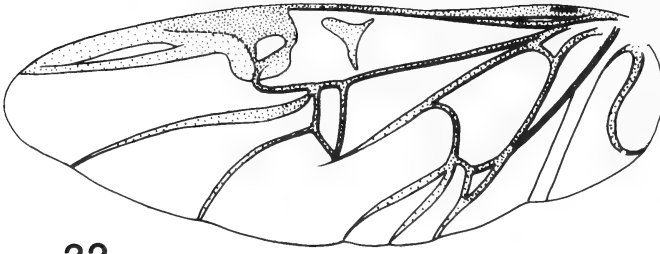
Figs. 1-8. Line drawings of mouthparts of adult Elaphrini. Figs. 1-4. Mandibles. 1. Mandible of *B. quadricollis* Haldeman, ventral aspect, a) right, b) left. 2. Right mandible of *D. polita* Faldermann, ventral aspect. 3. Right mandible of *E. lapponicus* Gyllenhal, a) ventral aspect, b) inner aspect. 4. Right mandible of *E. parviceps* Van Dyke, ventral aspect. Figs. 5-7. Maxillae, ventral aspect. 5. *D. polita* Faldermann. 6. *B. quadricollis* Haldeman. 7. *E. lapponicus* Gyllenhal. Fig. 8. Gula and labium of *D. polita* Faldermann, ventral aspect.



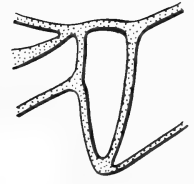
Figs. 9–17. Line drawings of structures of adult Elaphrini. Figs. 9–10. Gula and labium, ventral aspect. 9. *B. quadricollis* Haldeman. 10. *E. lapponicus* Gyllenahl. Figs. 11–13. Antennomeres 1–4, dorsal aspect. 11. *E. riparius* Linnaeus 12. *E. parviceps* Van Dyke. 13. *E. lecontei* Crotch. Figs. 14–16. Head, dorsal aspect. 14. *D. polita* Faldermann. 15. *B. multipunctata* Linnaeus. 16. *E. lapponicus* Gyllenahl. Fig. 17. Pronotum of *E. uliginosus* Fabricius, a) dorsal aspect, b) lateral aspect.



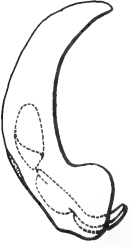
Figs. 18–31. Line drawings of pronota and elytra of adult Elaphrini. Fig. 18. Pronotum of *E. fuliginosus* Say, a) dorsal aspect, b) lateral aspect. Figs. 19–25. Pronotum, dorsal aspect. 19. *E. cupreus* Duftschmid. 20. *E. marginicollis* n. sp. 21. *E. mimus* n. sp. 22. *E. viridis* Horn. 23. *E. lheritieri* Antoine. 24. *E. lecontei* Crotch. 25. *E. riparius* Linnaeus. Figs. 26–27. Pronotum, lateral aspect. 26. *E. angusticollis angusticollis* Sahlberg 27. *E. purpurans* Hausen. Figs. 28–31. Elytral striae 2 (right) and 3 (left), discal portion. 28. *D. polita* Faldermann. 29. *B. eschscholtzi* Zoubkoff. 30. *B. quadricollis* Haldeman. 31. *E. lapponicus* Gyllenhal.



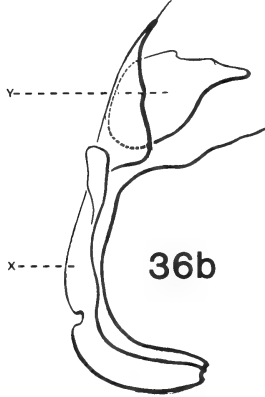
32



33



36a



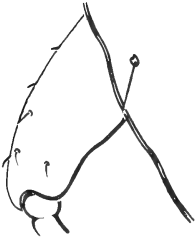
36b



36c



36d



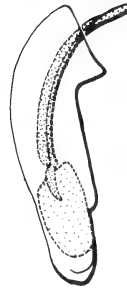
34



37c



37d



37a



37b



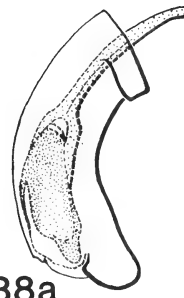
35



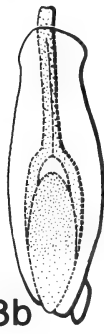
38c



38d

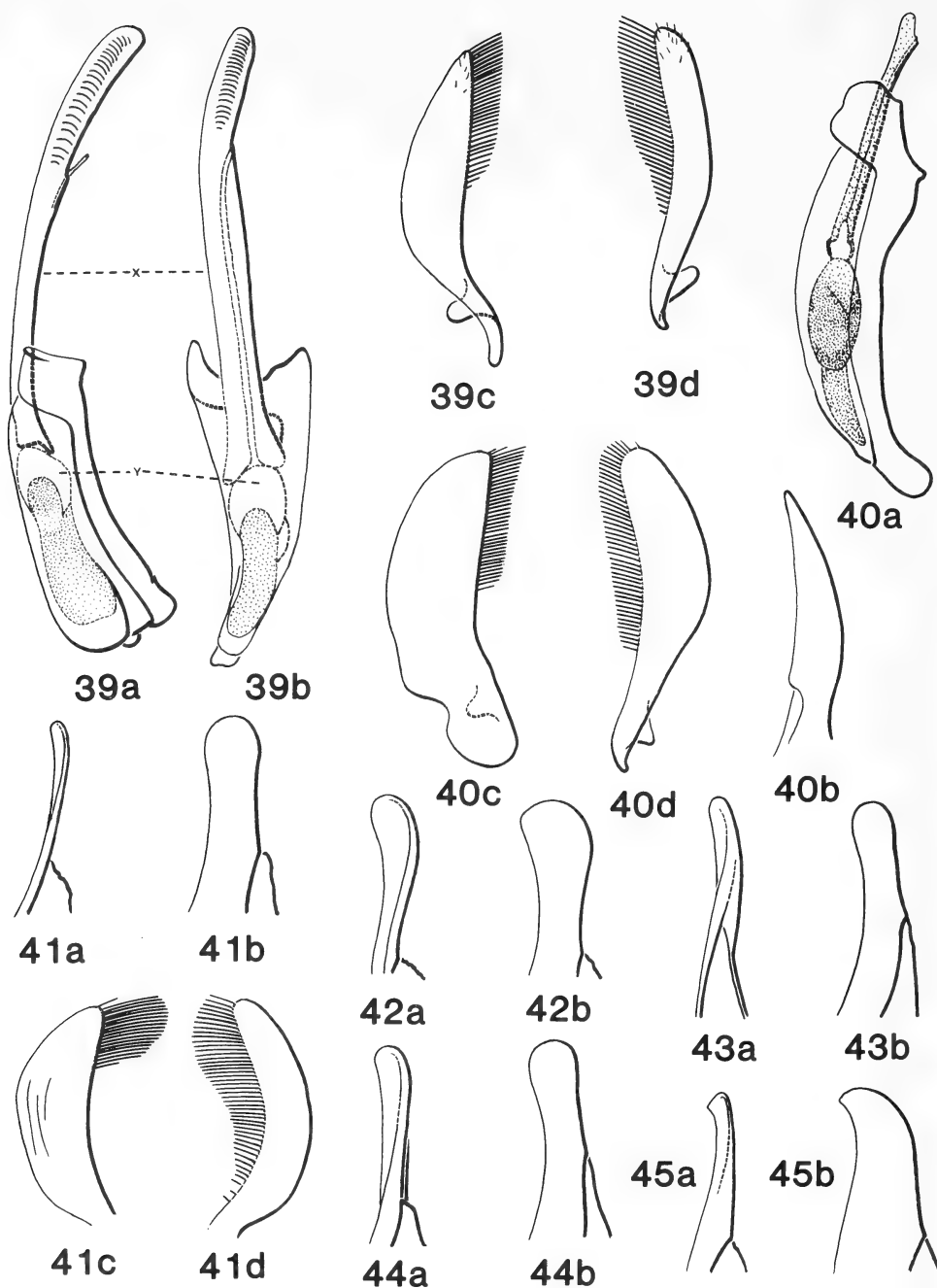


38a



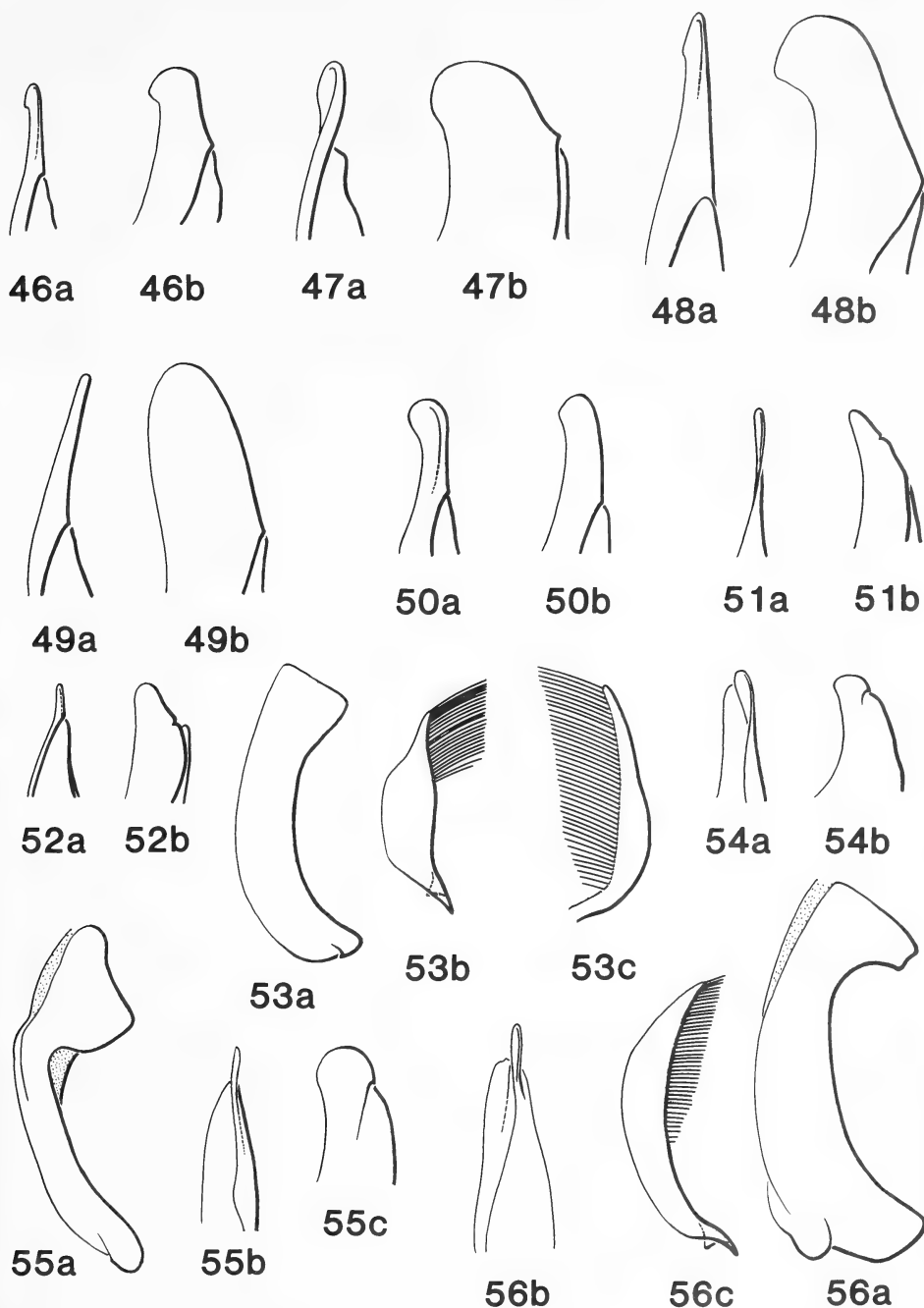
38b

Figs. 32–38. Line drawings of structures of adult Elaphrini. Figs. 32–33. Hindwing. 32. *E. americanus* Dejean. 33. Oblongum of *B. multipunctata* Linnaeus. Figs. 34–35. Dorso-subapical surface of hind femur. 34. *E. americanus* Dejean. 35. *E. californicus* Mannerheim. Fig. 36. Male genitalia of *Broscus cephalotes* (redrawn from Ball, 1956), a) median lobe lateral aspect, b) detail of internal sac (inverted) showing sclerites X and Y, lateral view, c) left paramere, d) right paramere. Figs. 37–38. Male genitalia, a) lateral aspect of median lobe and internal sac, b) dorsal aspect of median lobe and internal sac c) left paramere, d) right paramere. 37. *Melaenus piger*. 38. *D. arctica* Gyllenhal.

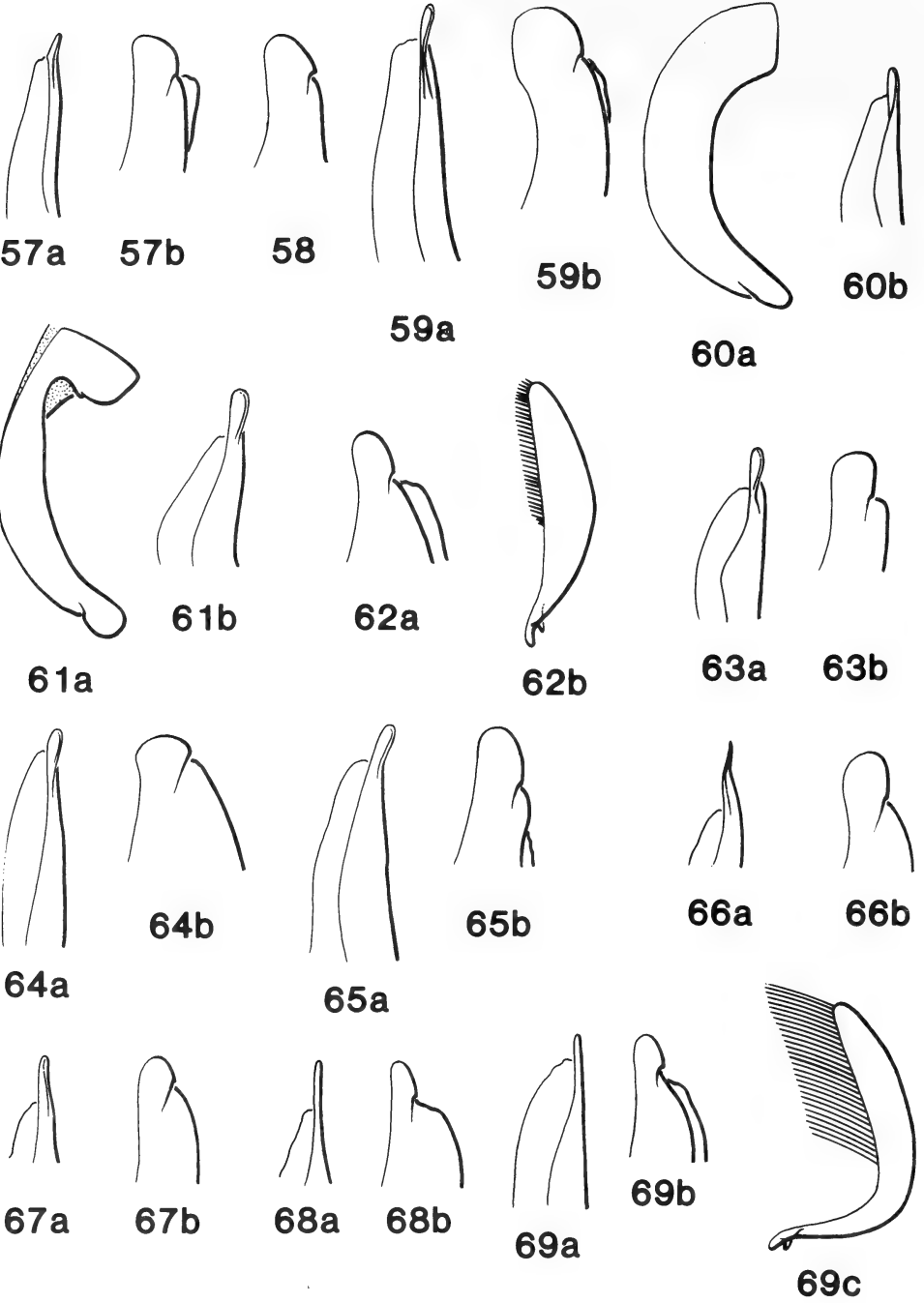


Figs. 39–45. Line drawings of male genitalia of adult Elaphrini. Figs. 39–40. Median lobe and internal sac, a) lateral aspect, b) dorsal aspect; c) left paramere, d) right paramere. 39. *B. multipunctata* Linnaeus. 40. *E. lapponicus obliteratus* Mannerheim. Fig. 41. *E. splendidus* Fischer von Waldheim. a) apex of median lobe, dorsal aspect, b) apex of median lobe, lateral aspect, c) left paramere, d) right paramere. Figs. 42–45. Apex of median lobe, a) dorsal aspect, b) lateral aspect. 42. *E. japonicus* Uéno. 43. *E. uliginosus* Fabricius. 44. *E. pyrenoeus* Motschulsky. 45. *E. fuliginosus* Say.

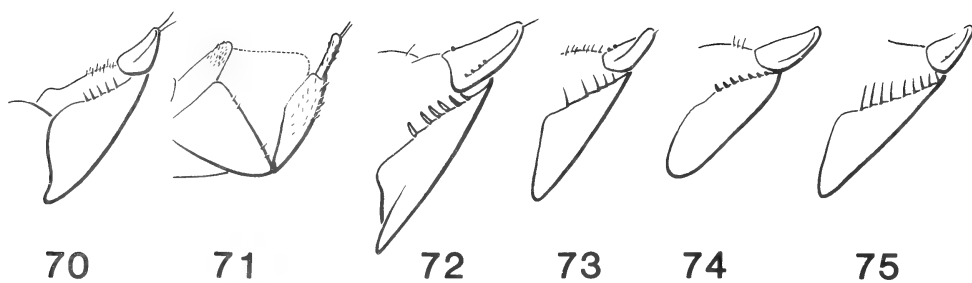




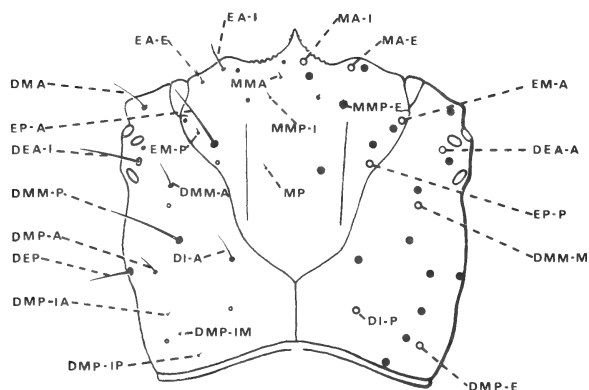
Figs. 46-56. Line drawings of male genitalia of adult Elaphrini. Figs. 46-52. Apex of median lobe, a) dorsal aspect, b) lateral aspect. 46. *E. lindrothi* n. sp. 47. *E. cicatricosus* LeConte. 48. *E. sibiricus* Motschulsky. 49. *E. cupreus* Duftschmid. 50. *E. clairvillei* Kirby. 51. *E. olivaceus* LeConte. 52. *E. laevigatus* LeConte. Fig. 53. *E. punctatus* Motschulsky, Japan, a) lateral aspect of median lobe, b) left paramere, c) right paramere. Fig. 54. Apex of median lobe of *E. punctatus* Motschulsky, Irkutsk, USSR, a) ventral aspect, b) lateral aspect. Fig. 55. Median lobe of *E. aureus* Müller, a) lateral aspect, b) ventral aspect of apex, c) lateral aspect of apex. Fig. 56. *E. purpurans* Hausen. a) lateral aspect of median lobe, b) ventral aspect of apex of median lobe, c) right paramere.



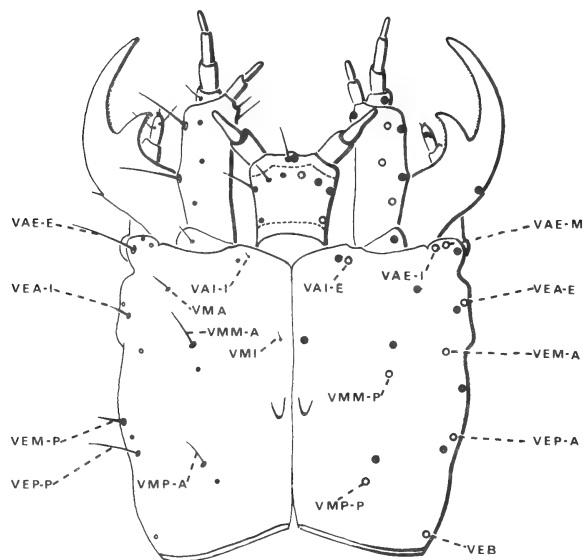
Figs. 57–69. Line drawings of male genitalia of adult Elaphrini. Fig. 57. Apex of median lobe of *E. angusticollis longicollis* Sahlberg, a) ventral aspect, b) lateral aspect. Fig. 58. Apex of median lobe of *E. angusticollis angusticollis* Sahlberg, . lateral aspect. Fig. 59. Apex of median lobe of *E. ulrichi* Redtenbacher, a) ventral aspect, b) lateral aspect. Figs. 60–61. Median lobe, a) lateral aspect, b) ventral aspect of apex. 60. *E. ruscarius* Say. 61. *E. riparius* Linnaeus. Fig. 62. *E. hypocrita* Semenov, a) lateral aspect of apex of median lobe, b) right paramere. Figs. 63–68. Apex of median lobe, a) ventral aspect, b) lateral aspect. 63. *E. comatus* n. sp., Harbin, China. 64. *E. lheritieri* Antoine. 65. *E. lecontei* Crotch. 66. *E. finitimus* Casey, Tocaloma, California. 67. *E. americanus* Dejean, Pullman, Washington. 68. *E. americanus* Dejean, Seattle, Washington. Fig. 69. *E. americanus* Dejean, Spring Creek Basin, Alberta, a) ventral aspect of median lobe, b) lateral aspect of median lobe, c) right paramere.



76a



76b



Figs. 70-75. Line drawings of ovipositor styli, lateral aspect, of adult Elaphrini. 70. *D. polita* Faldermann. 71. *B. multipunctata* Linnaeus. 72. *E. lapponicus obliteratus* Mannerheim. 73. *E. clairvillei* Kirby. 74. *E. purpurans* Hausen. 75. *E. lecontei* Crotch. Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, a) dorsal aspect of the head, b) ventral aspect of the head. Setae and pores represented by black and pen circles respectively on the right side of figure.

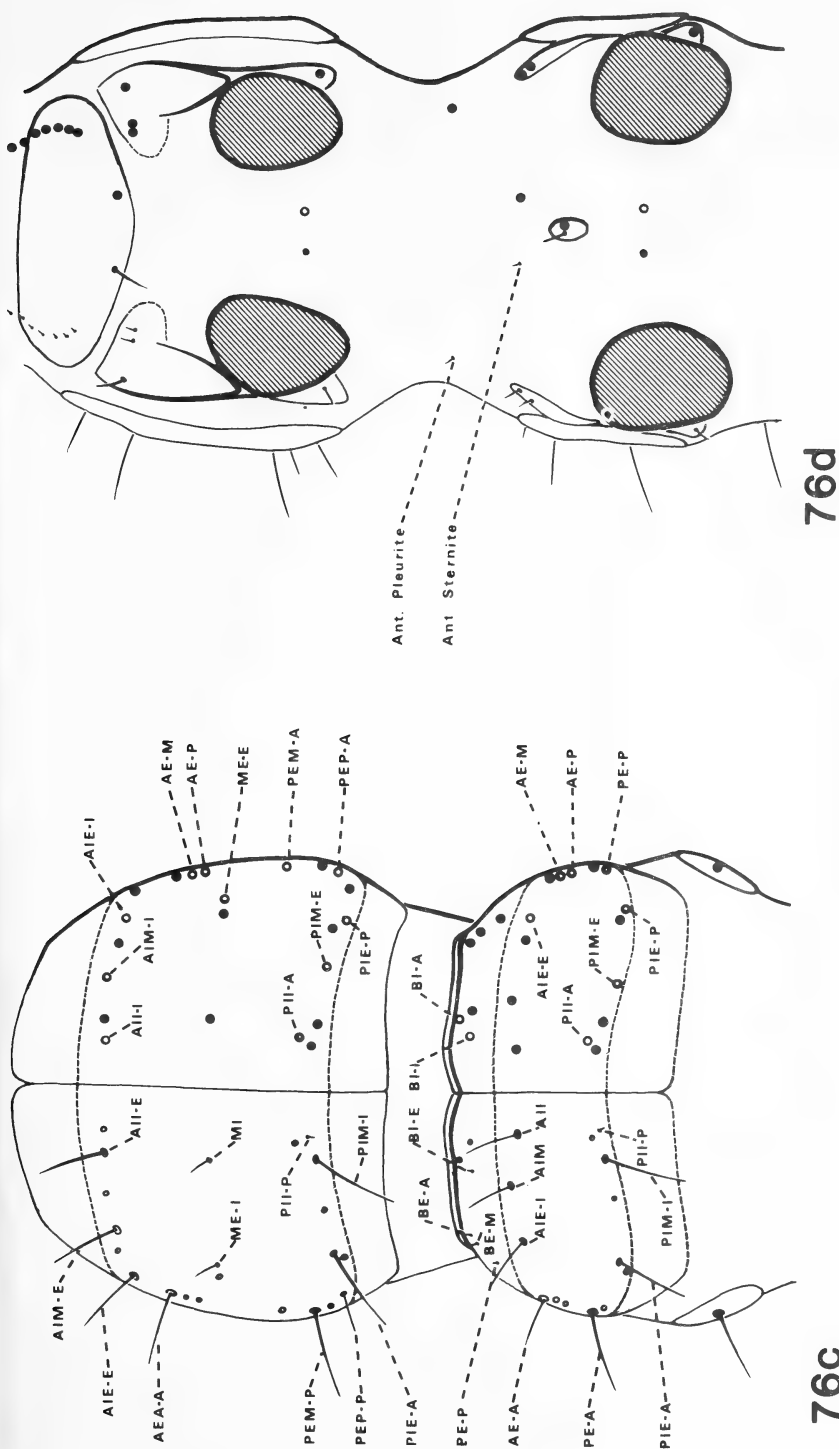


Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby. c) dorsal aspect of prothorax and mesothorax, d) ventral aspect of prothorax and mesothorax. Setae and pores symbolized respectively by black and open circles on the right side of figure. Pale portions of nota and terga are termed "bands". The anterior band is anterior of the subapical dashed line in Fig. 76c; the posterior band is posterior to the sub-basal dashed line in Fig. 76c; the lateral band is the lateral portion as in Fig. 76d.

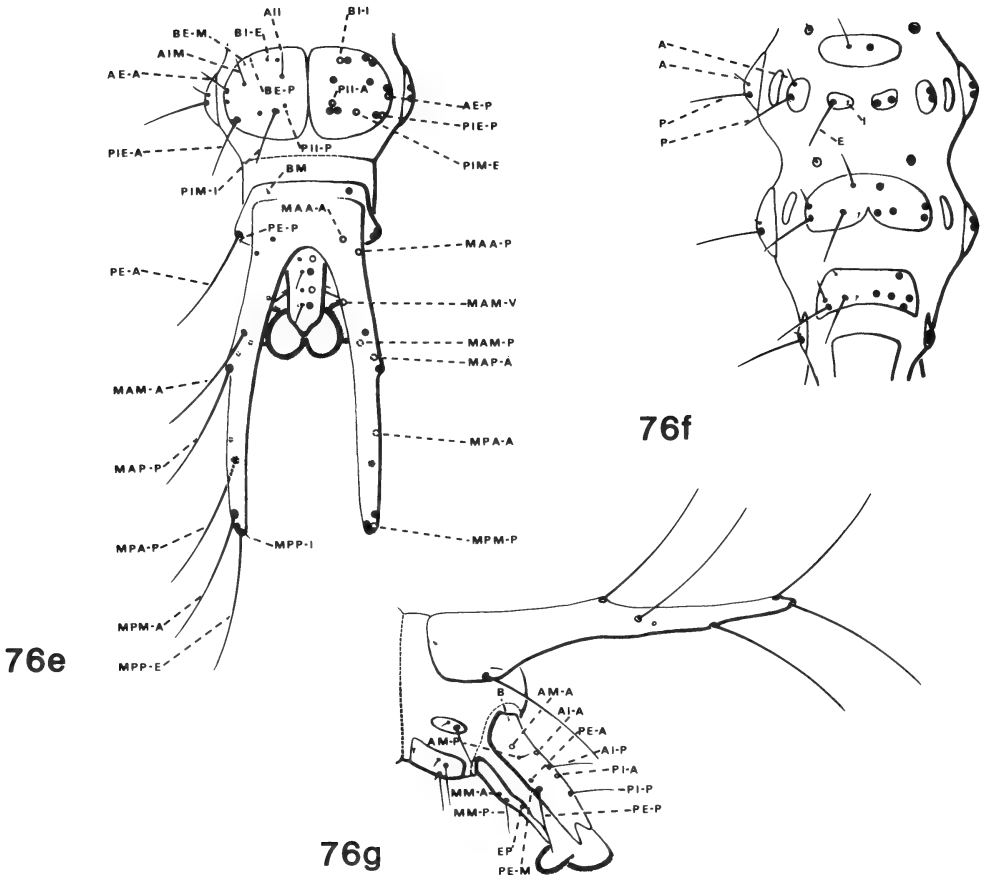
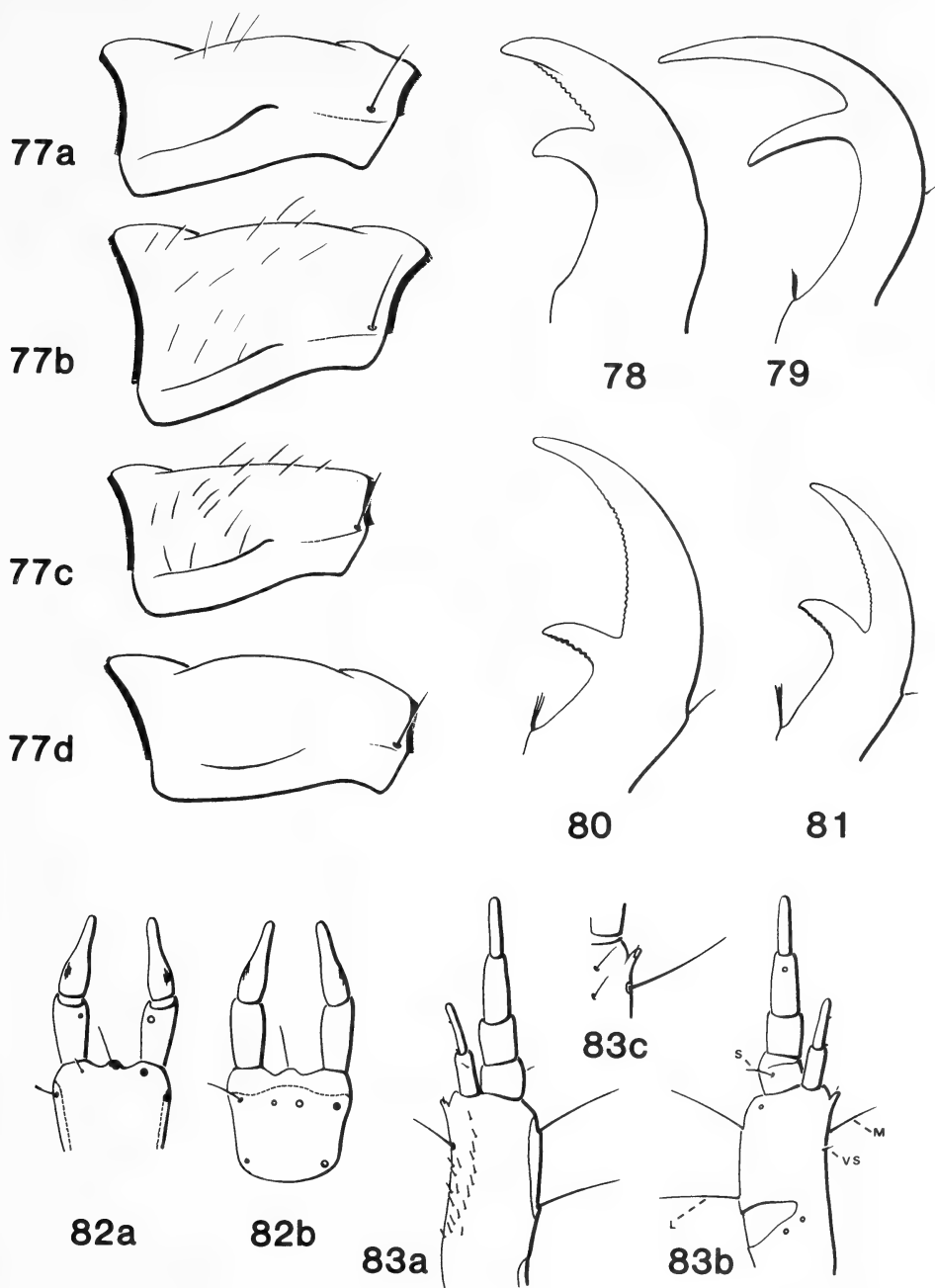


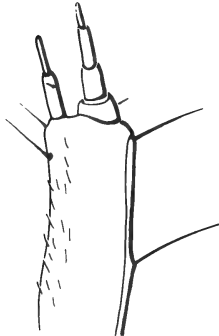
Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, e) dorsal aspect of abdominal segments 8, 9 and 10, f) ventral aspect of abdominal segments 7, 8 and 9, g) lateral aspect of abdominal segments 9 and 10. Setae and pores symbolized respectively by black and open circles on the right side of figure.



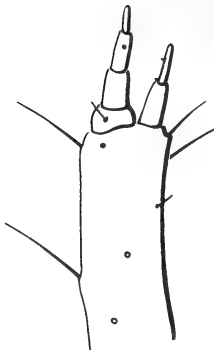
Figs. 77–83. Line drawings of structures of Elaphrini. Fig. 77. Lateral aspect of pronotum of adult a) *E. lheritieri* Antoine, b) *E. minus* n. sp., c) *E. viridis* Horn, d) *E. californicus* Mannerheim. Figs. 78–81 Mandibles. 78. Third instar larva of *D. arctica* Gyllenhal (redrawn from Lindroth, 1954). 79. First instar larva of *D. polita* Faldermann. 80. First instar larva of *E. clairvillei* Kirby. 81. First instar larva of *E. lecontei* Crotch. Fig. 82. Labium of first instar larva of *E. clairvillei* Kirby, a) dorsal aspect, b) ventral aspect. Fig. 83. Maxilla of first instar larva of *D. polita* Faldermann, a) dorsal aspect, b) ventral aspect, c) lacinia. L = large seta, M = medium-sized seta, S = small seta, VS = very small seta.



84



85a



85b



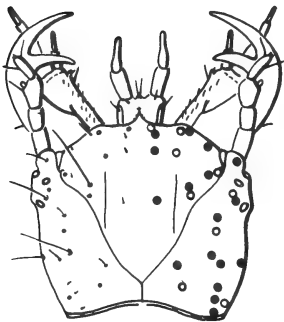
85c



87b



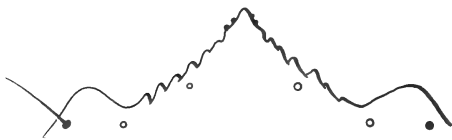
86



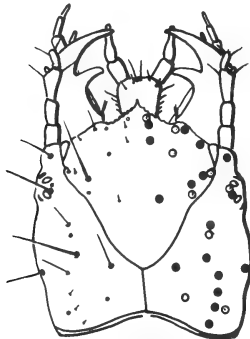
87a



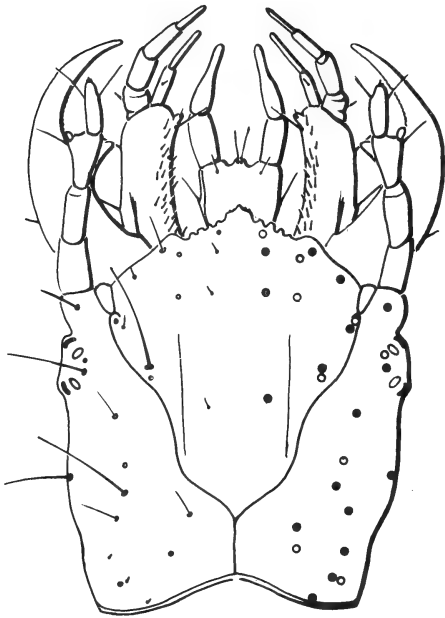
88b



89b



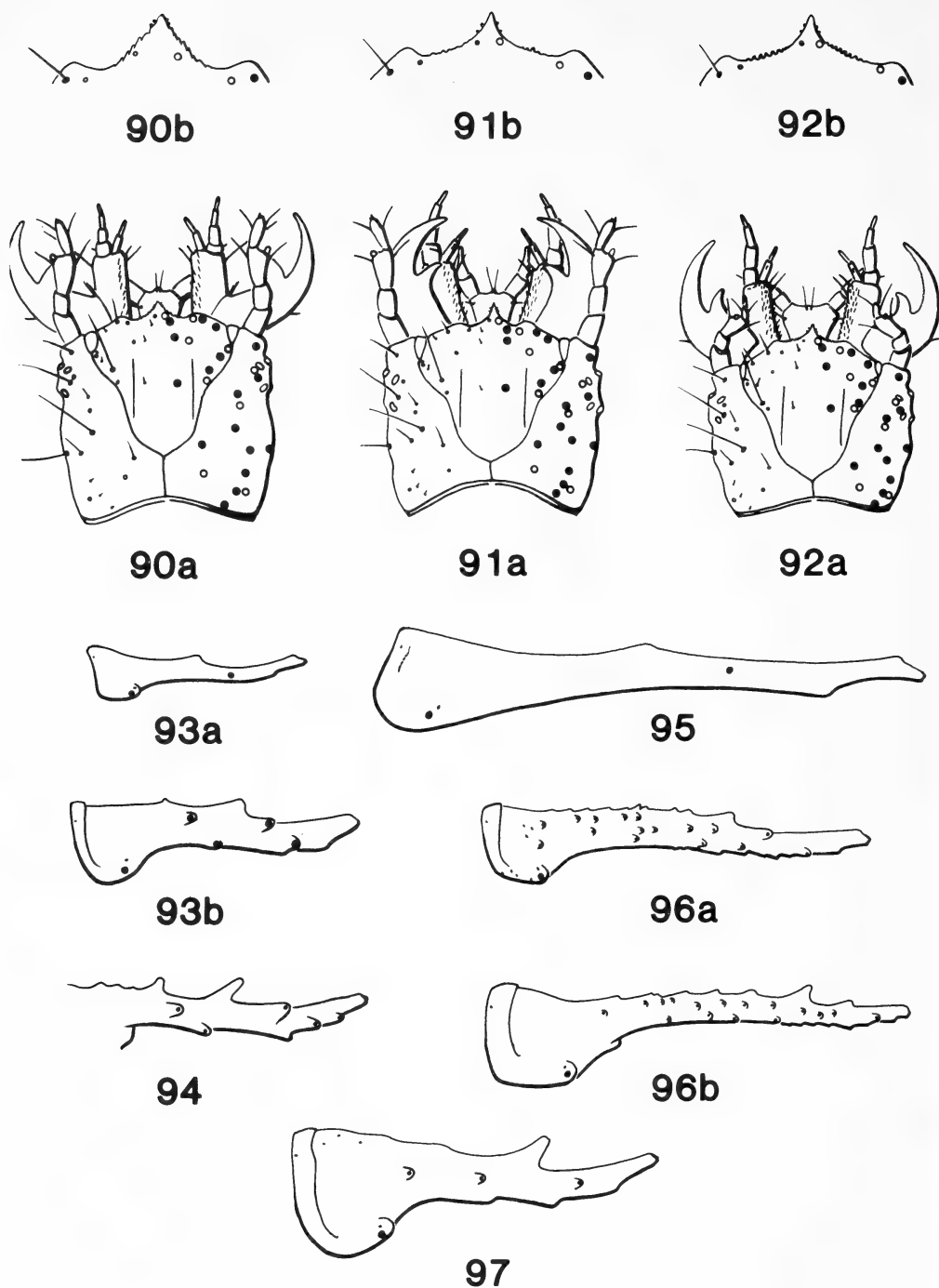
89a



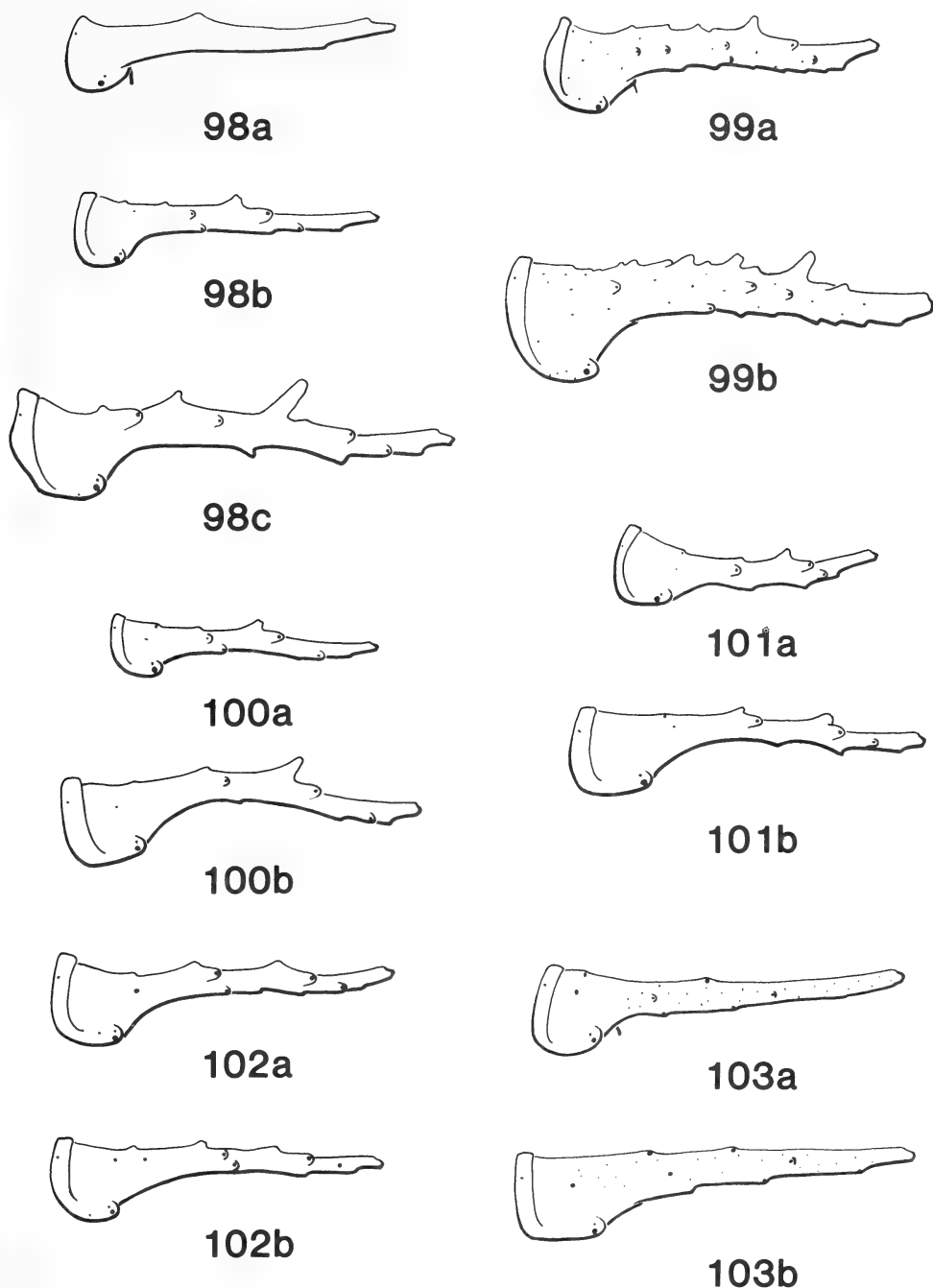
88a



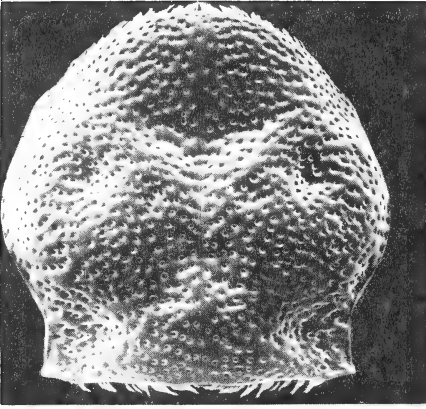
Figs. 84–89. Line drawings of head and mouthparts of larval Elaphrini. Fig. 84. Lacinia of *D. arctica* Gyllenhal (redrawn from Lindroth, 1954). Fig. 85. Maxilla of *E. clairvillei* Kirby, a) dorsal aspect, b) ventral aspect, c) lacinia. Fig. 86. Lacinia of *E. purpurans* Hausen. Figs. 87–89. Head, a) dorsal aspect, b) nasale. 87. *D. polita* Faldermann. 88. *B. quadricollis* Haldeman. 89. *E. lapponicus lapponicus* Gyllenhal.



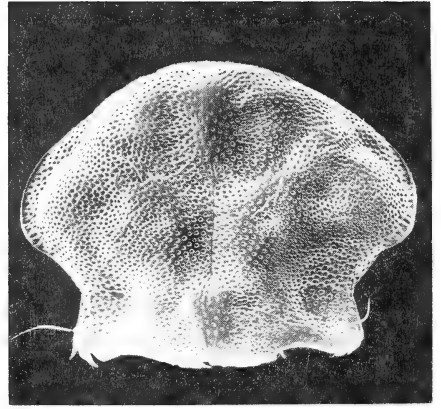
Figs. 90-97. Line drawings of structures of larval Elaphrini. Figs. 90-92. Head, a) dorsal aspect, b) nasale. 90. *E. clairvillei* Kirby. 91. *E. lecontei* Crotch. 92. *E. purpurans* Hausen. Figs. 93-97. Abdominal tergum 9, lateral aspect. 93. *D. polita* Faldermann, a) first, b) second instar larva. 94. *D. arctica* Gyllenhal, third instar larva. 95. *B. quadricollis* Haldeman, first instar larva. 96. *B. multipunctata* Linnaeus, a) second, b) third instar larva. 97. *E. lapponicus lapponicus* Gyllenhal, third instar larva.



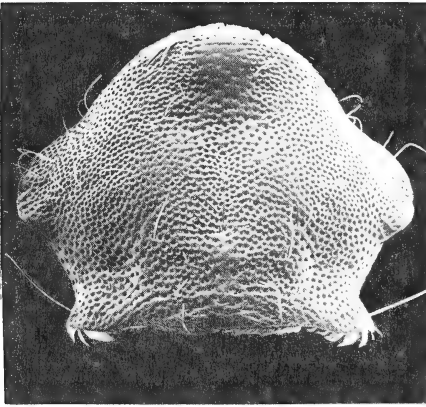
Figs. 98–103. Line drawings of abdominal tergum 9, lateral aspect, of larval Elaphrini. 98. *E. clairvillei* Kirby, a) first, b) second, c) third instar larva. 99. *E. cicatricosus* LeConte, a) second, b) third instar larva. 100. *E. americanus* Dejean, a) second, b) third instar larva. 101. *E. aureus* Müller, a) second, b) third instar larva. 102. *E. purpurans* Hausen, third instar larva, a) McMinnville, Oregon, b) Conjuring Creek, Alberta. 103. *E. ulrichi* Redtenbacher, a) second, b) third instar larva.



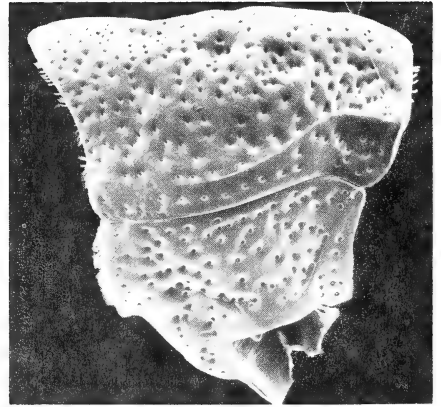
104



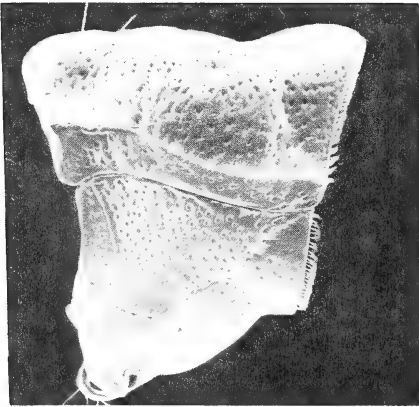
105



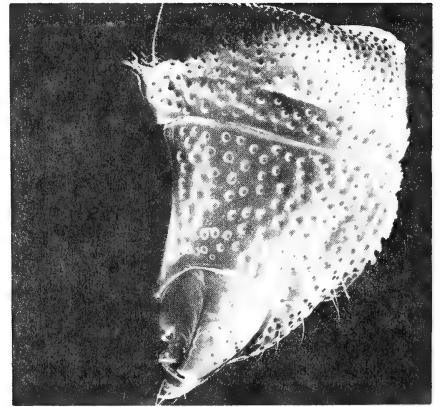
106



107



108

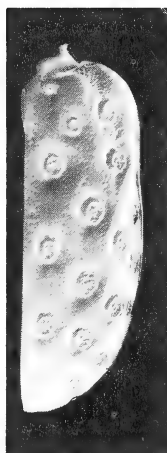


109

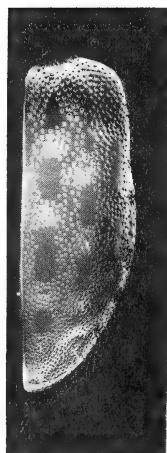
Figs. 104–109. Scanning electron micrographs of prothoraces of adult Elaphrini. Figs. 104–106. Pronotum, dorsal aspect. 104. *E. lindrothi* n. sp. 105. *E. lheritieri* Antoine. 106. *E. viridis* Horn. Figs. 107–109. Pronotum and prosternum, lateral aspect. 107. *E. cicatricosus* LeConte. 108. *E. cupreus* Duftschmid. 109. *E. ruscarius* Say.



110



111



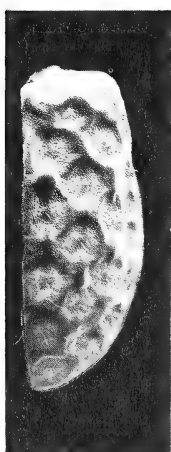
112



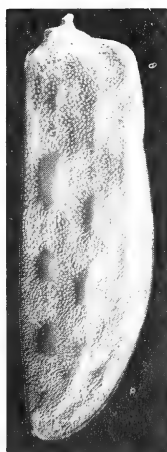
113



114



115



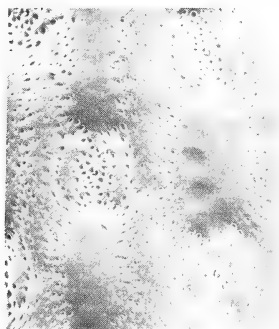
116



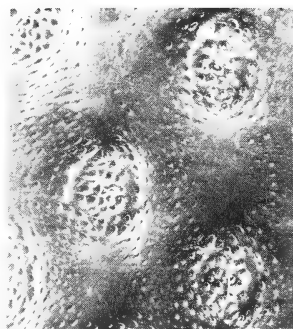
117



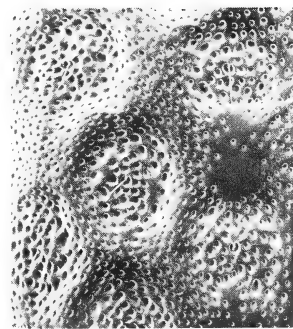
118



119

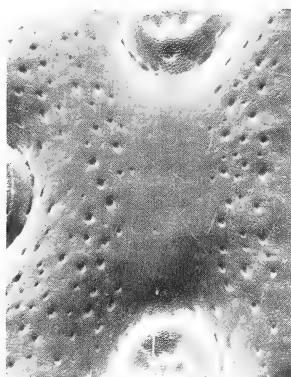


120

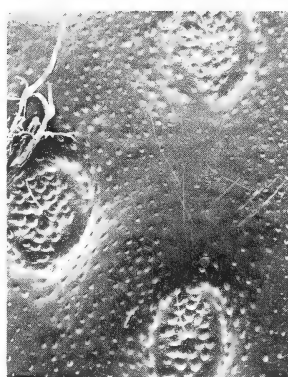


121

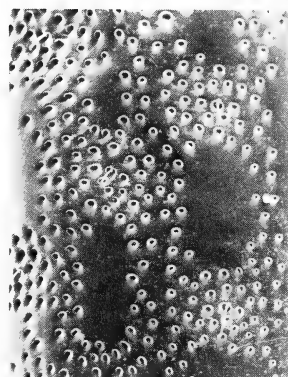
Figs. 110–121. Scanning electron micrographs of structures of adult Elaphrini. Figs. 110–117. Elytra. 110. *E. lapponicus lapponicus* Gyllenhal. 111. *E. clairvillei* Kirby. 112. *E. punctatus* Motschulsky, Japan. 113. *E. angusticollis angusticollis* Sahlberg. 114. *E. viridis* Horn. 115. *E. lheritieri* Antoine. 116. *E. parviceps* Van Dyke. 117. *E. americanus* Dejean, George Lake, Alberta. Figs. 118–121. Elytral pits on interval 3 (right) and 5, discal portion. 118. *E. lapponicus obliteratus* Mannerheim. 119. *E. uliginosus* Fabricius. 120. *E. pyrenoeus* Motschulsky. 121. *E. lindrothi* n. sp.



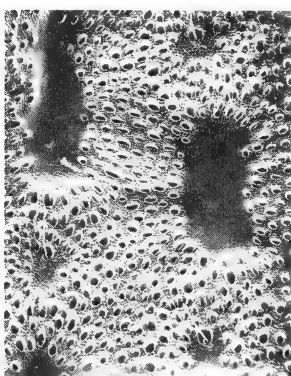
122



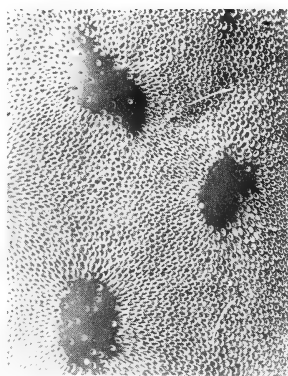
123



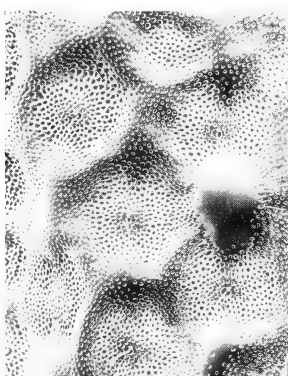
124



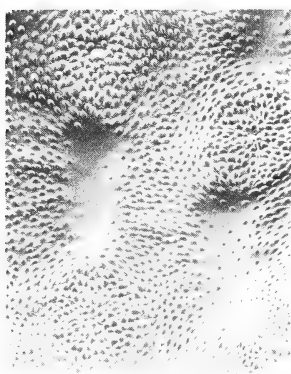
125



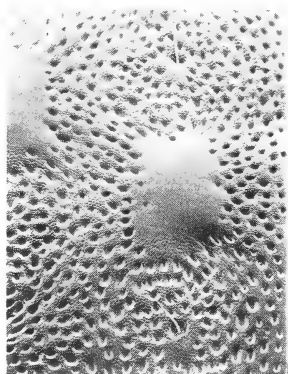
126



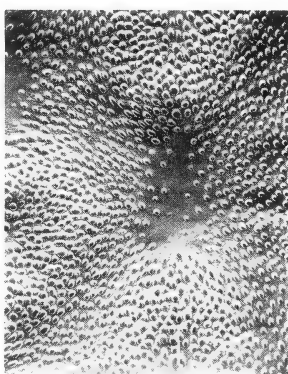
127



128



129



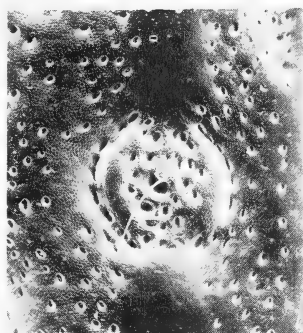
130

Figs. 122–130. Scanning electron micrographs of elytral pits on interval 3 (right) and 5, discal portion of adult Elaphrini. 122. *E. clairvillei* Kirby, George Lake, Alberta. 123. *E. olivaceus* LeConte. 124. *E. punctatus* Motschulsky, Japan. 125. *E. angusticollis angusticollis* Sahlberg. 126. *E. viridis* Horn. 127. *E. lheritieri* Antoine. 128. *E. americanus* Dejean, George Lake, Alberta. 129. *E. parviceps* Van Dyke. 130. *E. lecontei* Crotch, Pakowki Lake, Alberta.

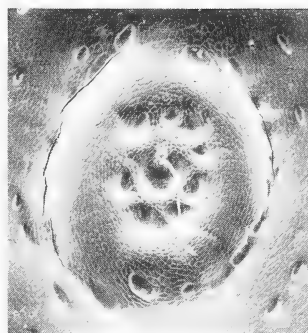




131



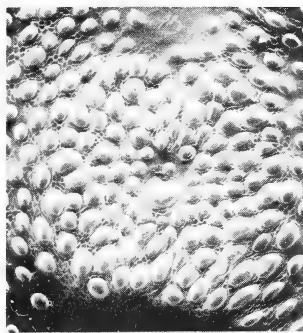
132



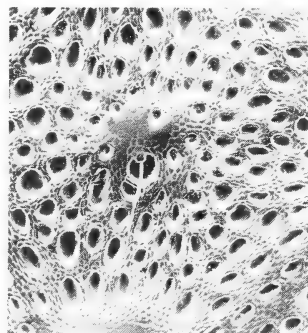
133



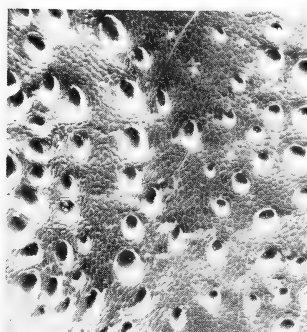
134



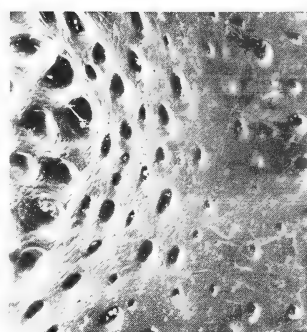
135



136

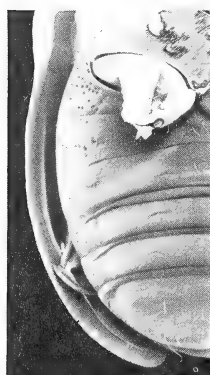


137

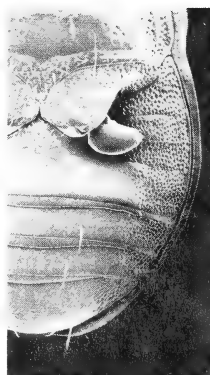


138

Figs. 131–138. Scanning electron micrographs of elytral sculpture of adult Elaphrini. Figs. 131–136. First sutural pit of elytron. 131. *E. lapponicus oblitteratus* Mannerheim. 132. *E. cupreus* Duftschmid. 133. *E. clairvillei* Kirby. 134. *E. olivaceus* LeConte. 135. *E. americanus* Dejean, George Lake, Alberta. 136. *E. parviceps* Van Dyke. Figs. 137–138. Microsculpture on elytral interval 4. 137. *E. uliginosus* Fabricius. 138. *E. pyrenoeus* Motschulsky.



139



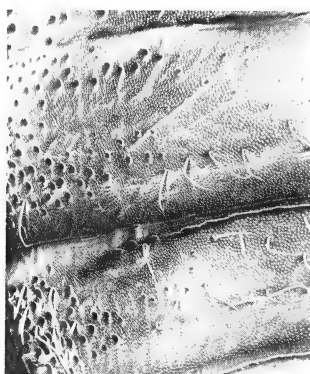
140



141



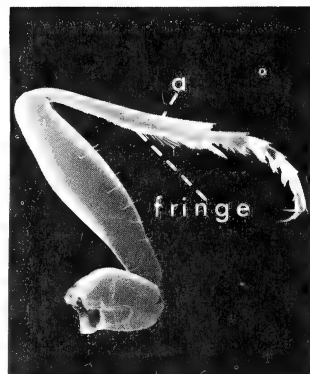
142



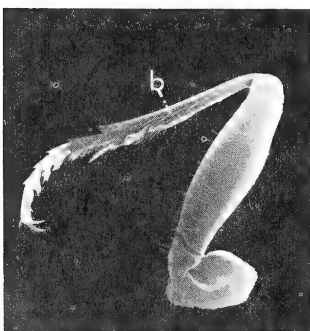
143



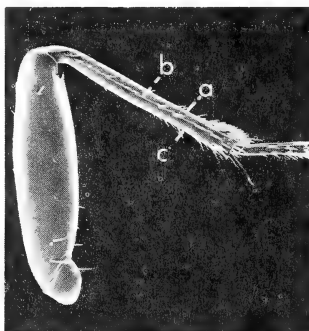
144



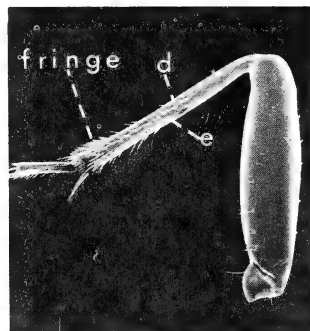
145



146

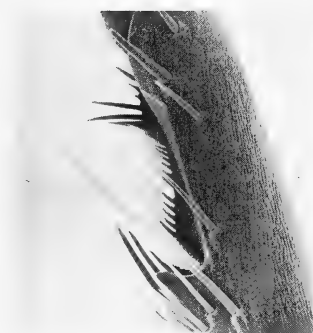


147

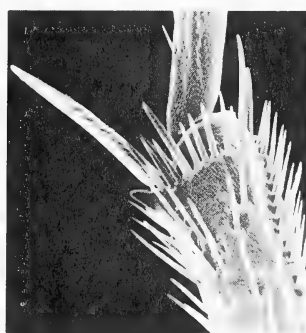


148

Figs. 139–148. Scanning electron micrographs of abdominal sterna and legs of adult Elaphrini. Figs. 139–142. Abdominal sterna. 139. *E. cicatricosus* LeConte. 140. *E. californicus* Mannerheim. 141. *E. riparius* Linnaeus. 142. *E. parviceps* Van Dyke. Figs. 143–144. Microsculpture on abdominal sterna 4 and 5. 143. *E. riparius* Linnaeus. 144. *E. parviceps* Van Dyke. Figs. 145–146. Foreleg of *E. cicatricosus* LeConte. 145. Anterior aspect. 146. Posterior aspect. Figs. 147–148. Midleg of *E. cicatricosus* LeConte. 147. Anterior aspect. 148. Posterior aspect.



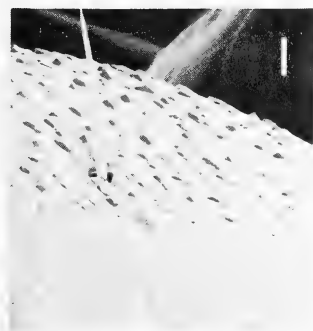
149



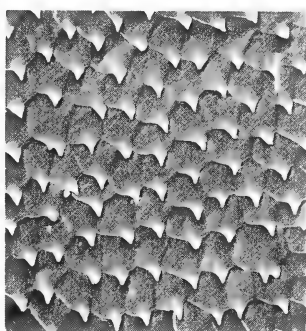
150



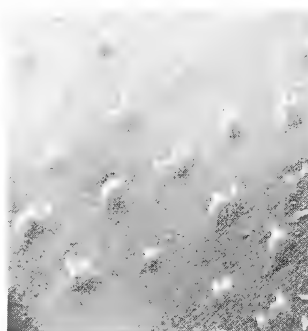
151



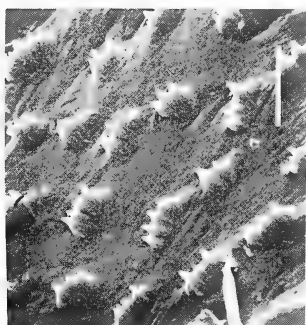
152



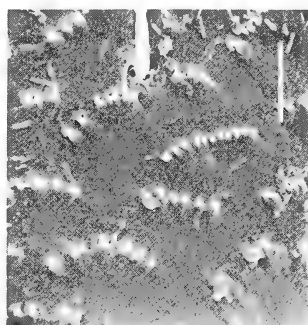
153



154



155



156

Figs. 149–156. Scanning electron micrographs of structures of Elaphrini. Figs. 149–150. Male adults of *E. cicatricosus* LeConte. 149. Apex of foreleg, posterior aspect. 150. Apex of midleg, posterior aspect. Figs. 151–156. Types of microsculpture (scale bar = 10 microns). 151. Isodiametric microsculpture, upper half smooth, lower half punctate (brown areas)—based on third instar larva of *E. angusticollis angusticollis* Sahlberg. 152. Scale-like microsculpture on side of head of third instar larva of *E. angusticollis angusticollis* Sahlberg. 153. Sharp scale-like microsculpture on abdominal sterna of adult *E. riparius* Linnaeus. 154. Single, double and triple-pointed microsculpture on tergum of third instar larva of *E. californicus* Mannerheim. 155. Raised multipointed microsculpture on abdominal sternum of third instar *E. californicus* Mannerheim. 156. Fine multi-pointed microsculpture on abdominal epipleuron of third instar larva of *E. angusticollis angusticollis* Sahlberg.

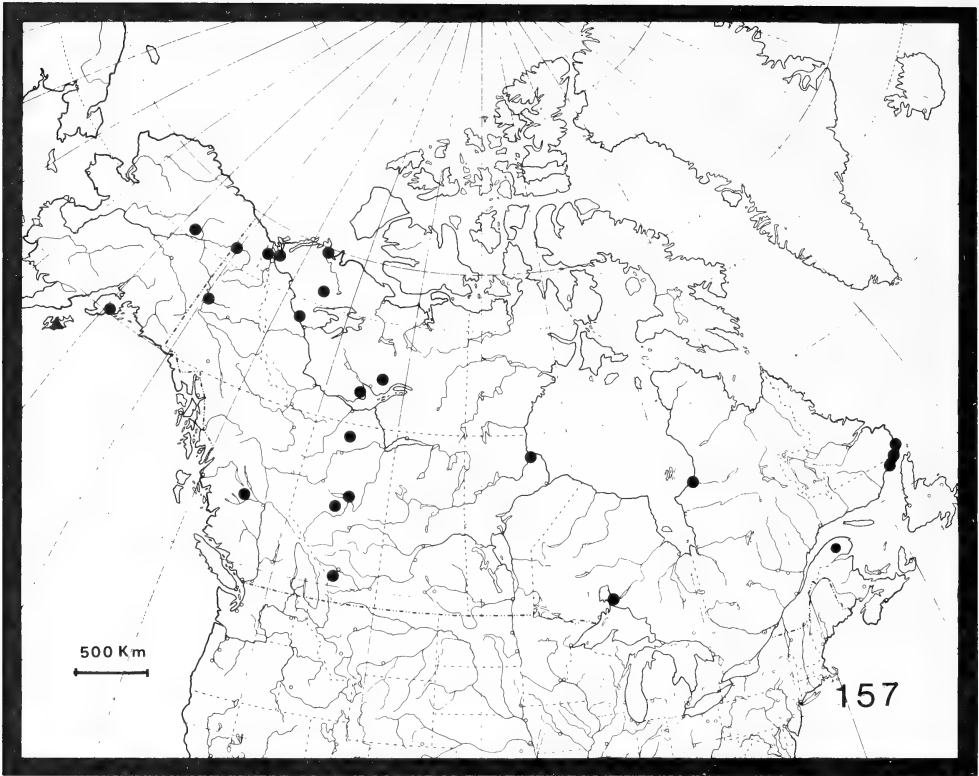
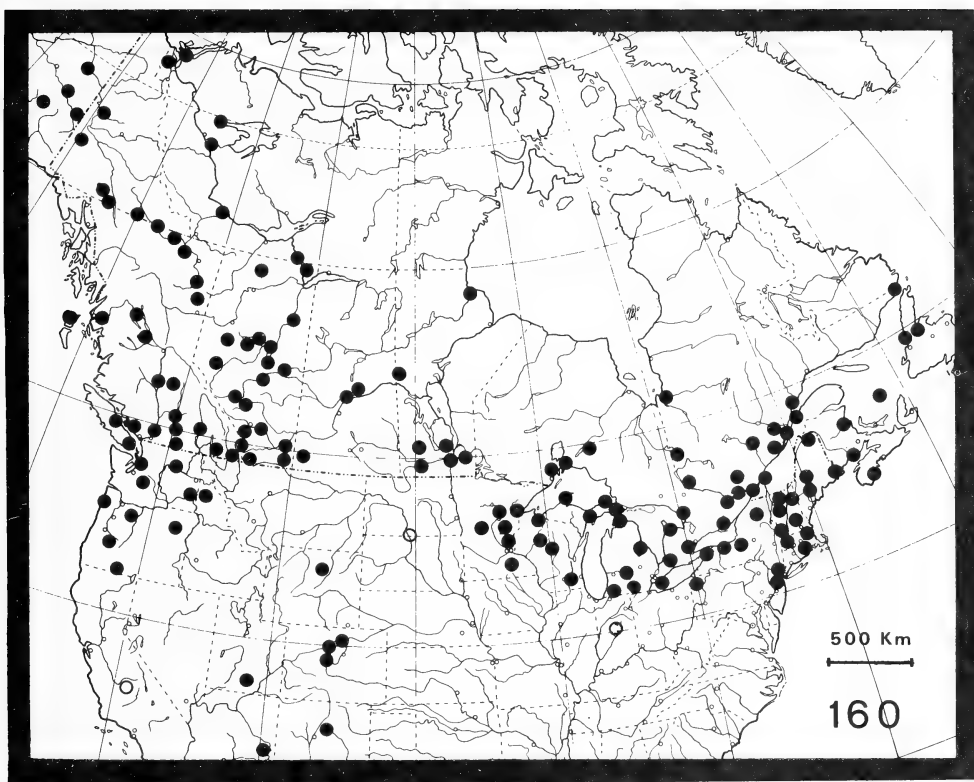
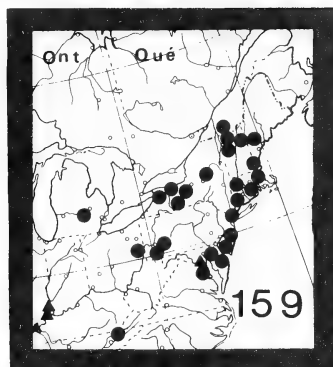
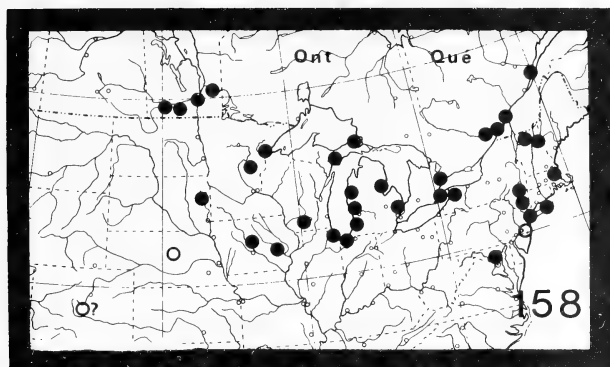


Fig. 157. Known distribution of *E. lapponicus lapponicus* Gyllenhal (circles) and *E. l. obliterated* Mannerheim (triangle) in North America.



Figs. 158–160. Known distribution. 158. *E. fuliginosus* Say. 159. *E. cicatricosus* LeConte (circles), and *E. lindrothi* n. sp. (triangles). 160. *E. clairvillei* Kirby.

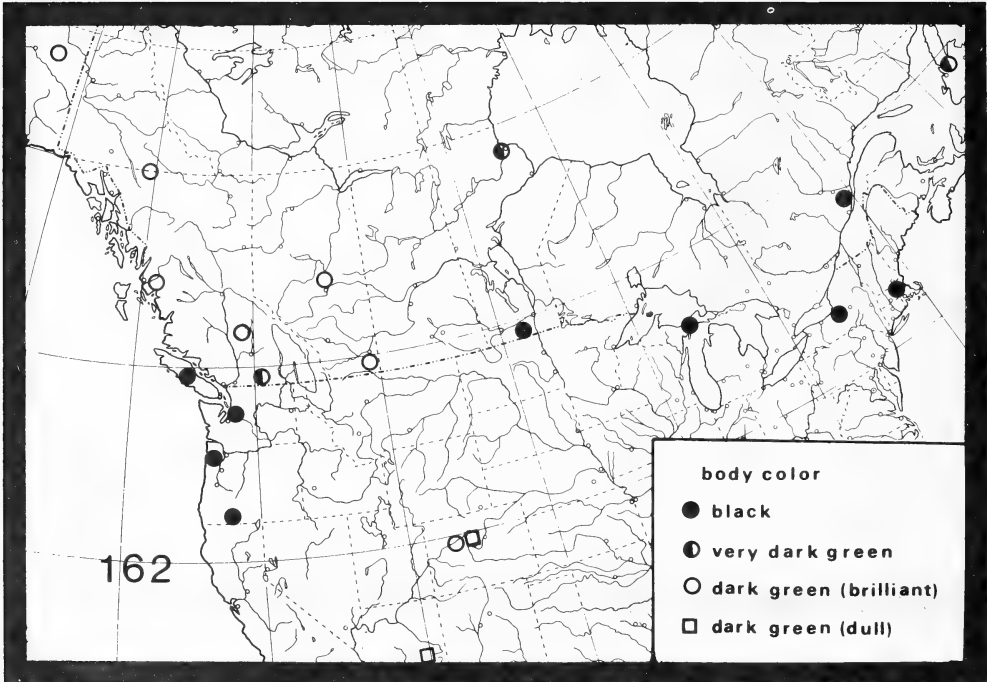
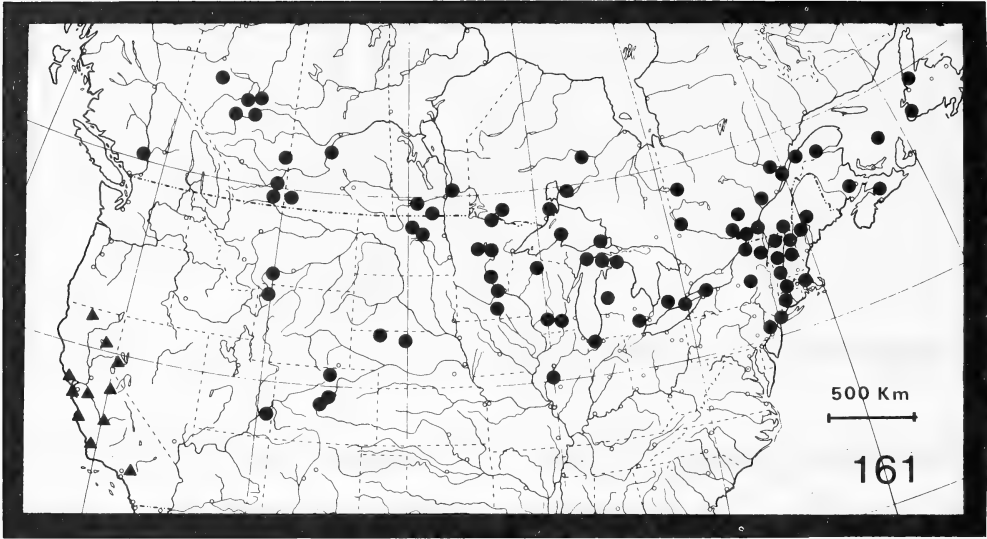
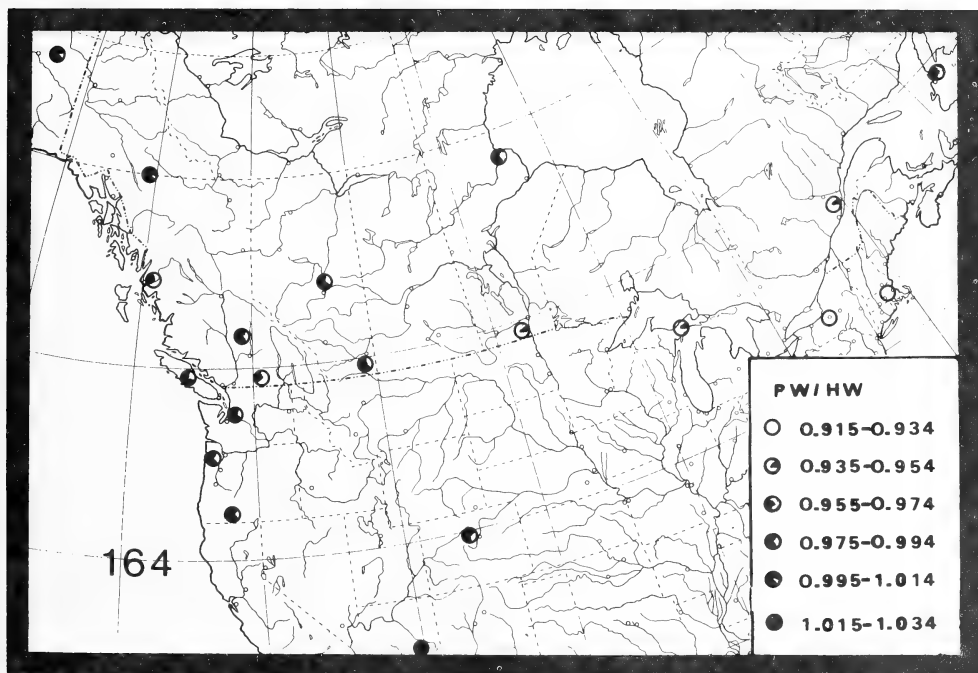
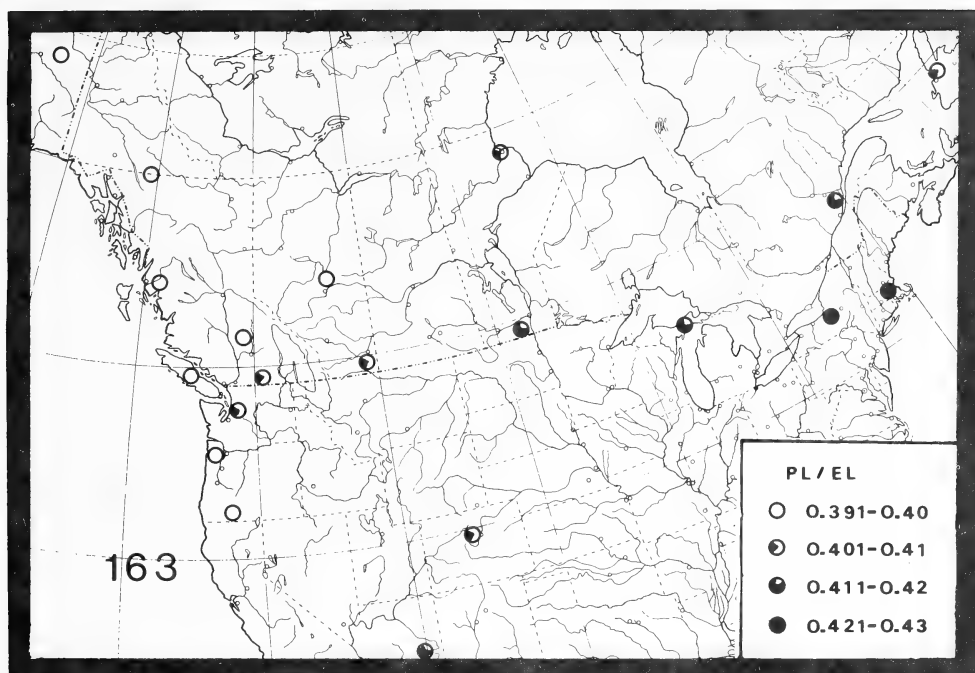
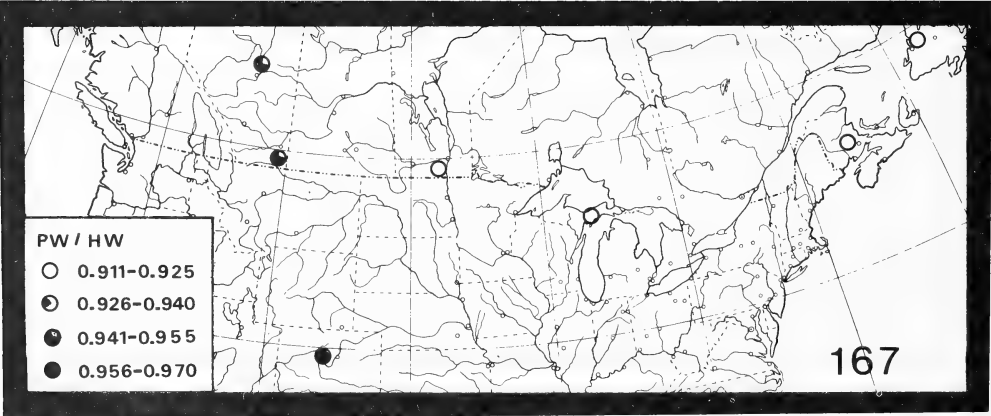
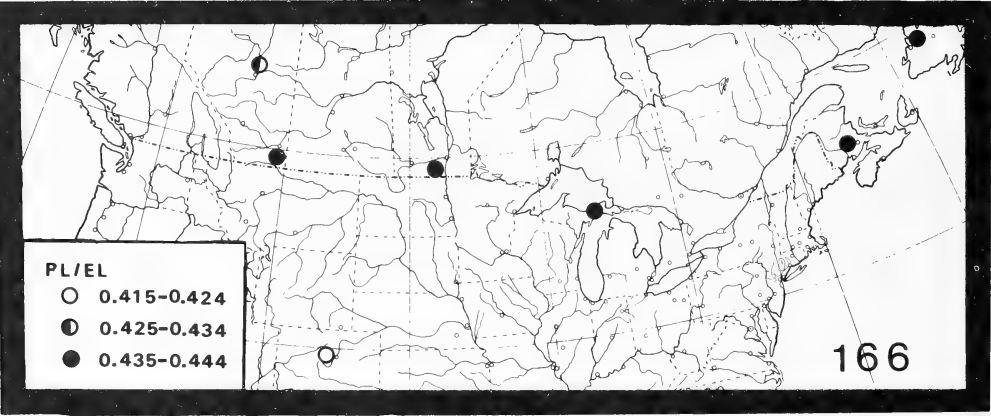
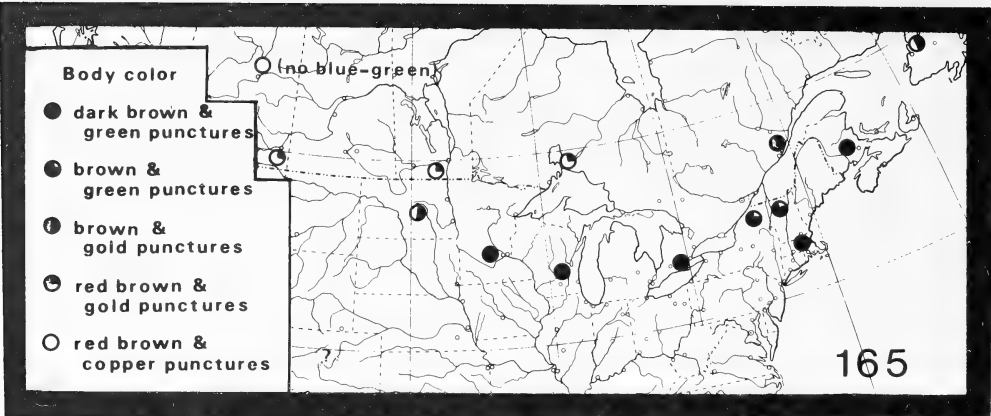


Fig. 161. Known distribution of *E. olivaceus* LeConte (circles) and *E. laevigatus* LeConte (triangles). Fig. 162. Variation in dorsal color of adults of *E. clairvillei* Kirby.

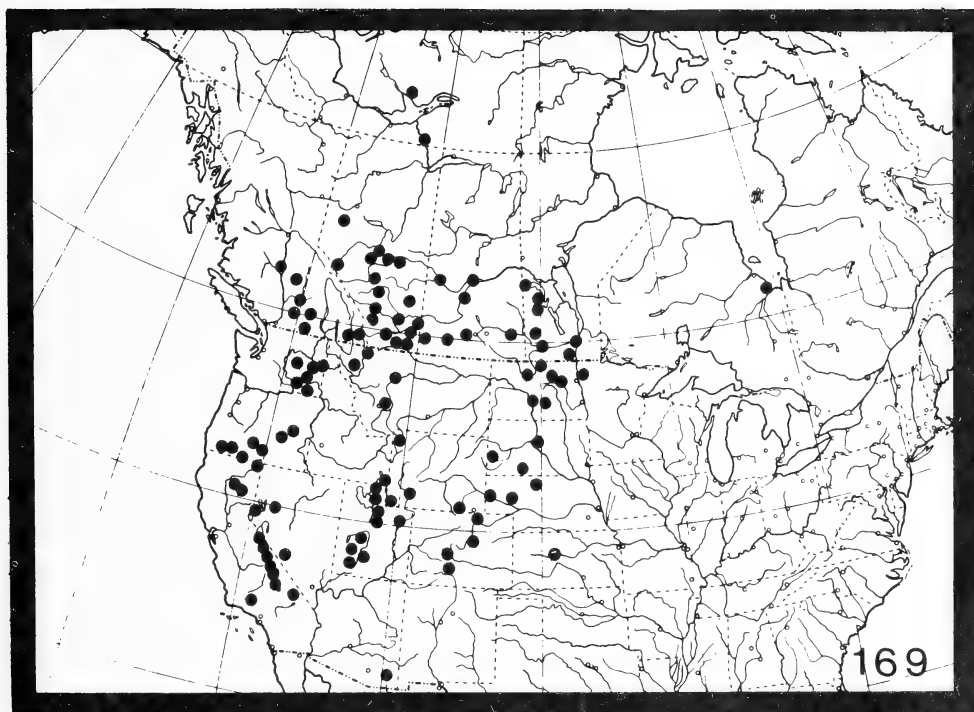
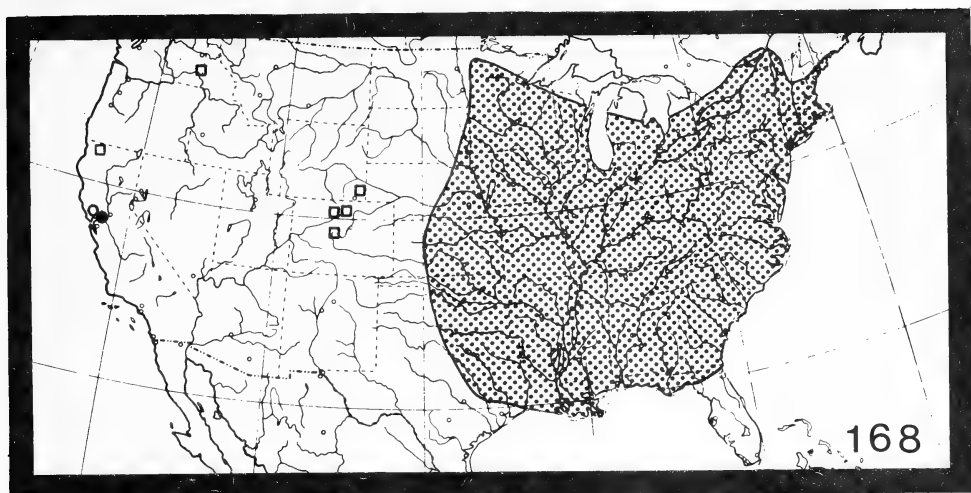


Figs. 163-164. Variation, based on adults of *E. clairvillei* Kirby. 163. Ratio PL/EL. 164. Ratio PW/HW.



Figs. 165-167. Variation, based on adults of *E. olivaceus* LeConte. 165. Variation of dark form. 166. Ratio PL/EL. 167. Ratio PW/HW.





Figs. 168–169. Known distribution. 168. *E. marginicollis* n. sp. (open squares), *E. mimus* n. sp. (open circle), *E. viridis* Horn (black circles), and *E. ruscarius* Say (stippled surface). 169. *E. lecontei* Crotch.

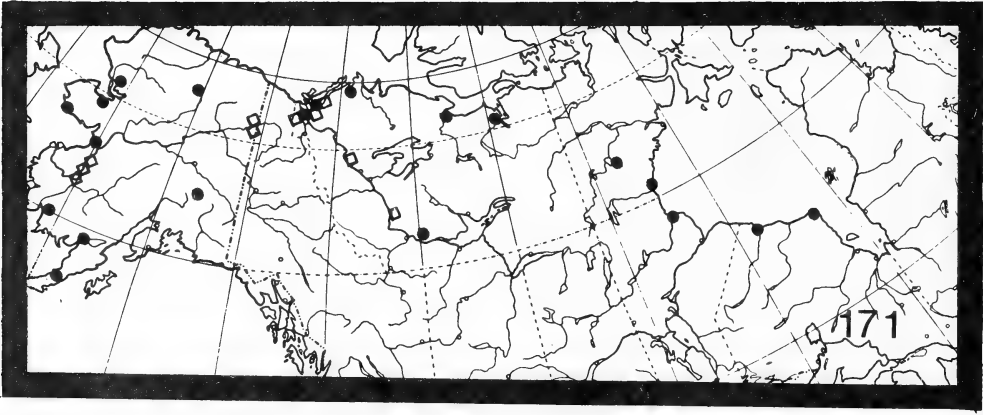
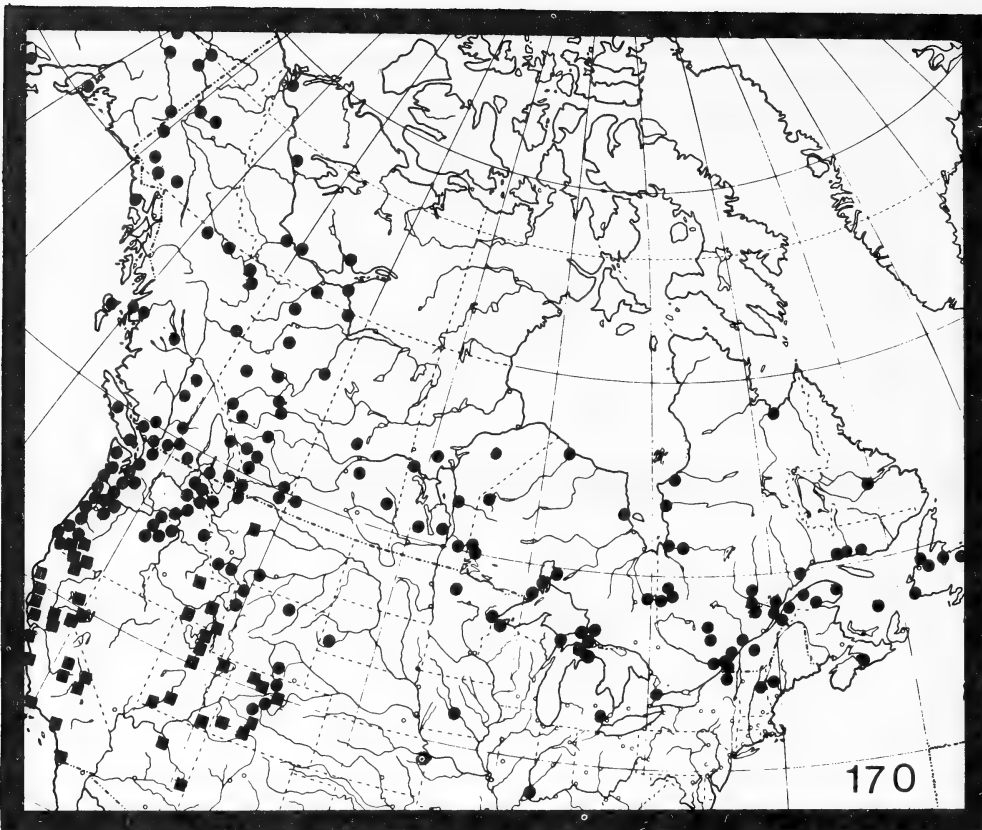
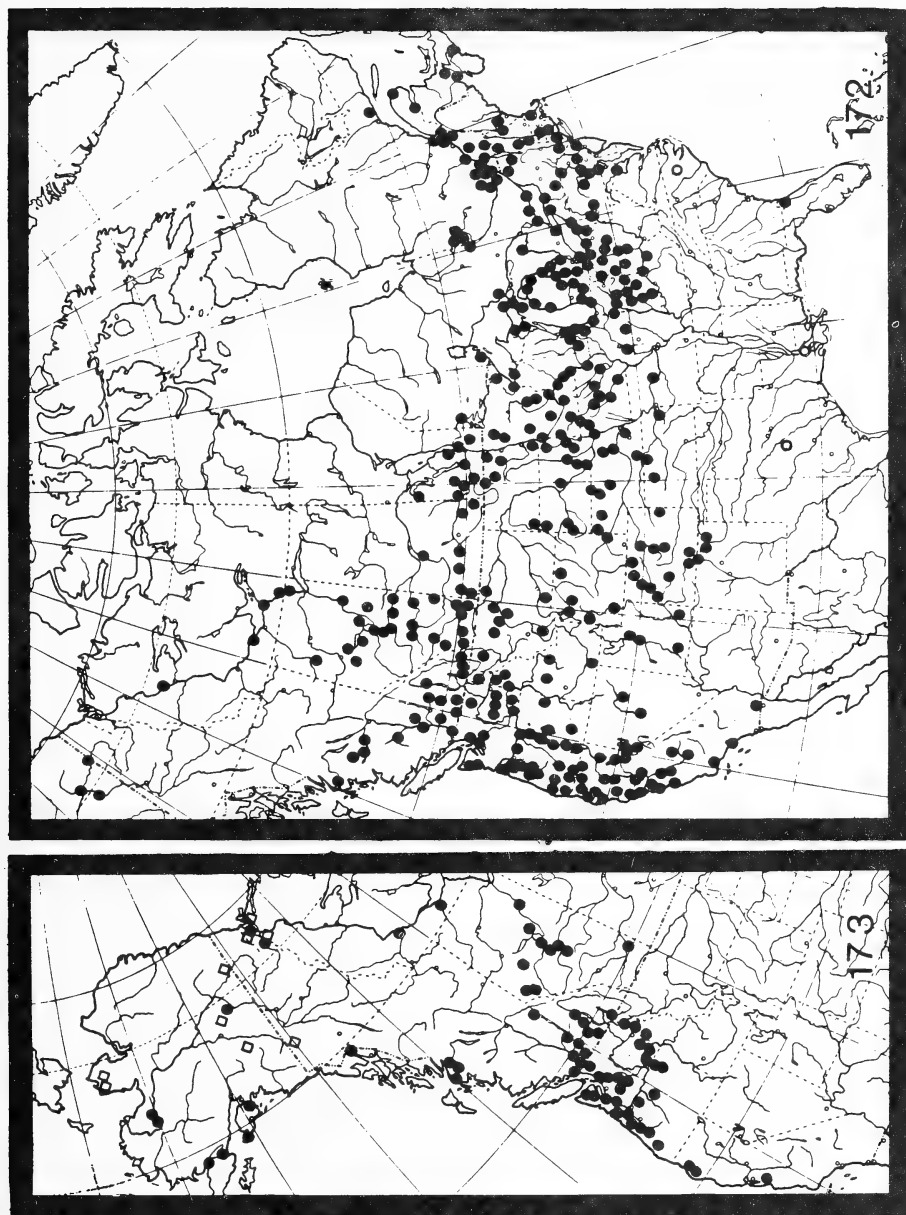


Fig. 170. Known distribution of *E. americanus* Kirby (circles) and *E. finitimus* Casey (squares). Fig. 171. Known Nearctic distribution of *E. tuberculatus* Mäklin (squares) and *E. parviceps* Van Dyke (circles).



Figs. 172-173. Known distribution. 172. *E. californicus* Mannerheim—state records noted as open circles. 173. *E. purpurans* Hausen (black circles) and *E. angusticollis* Sahlberg (open squares).

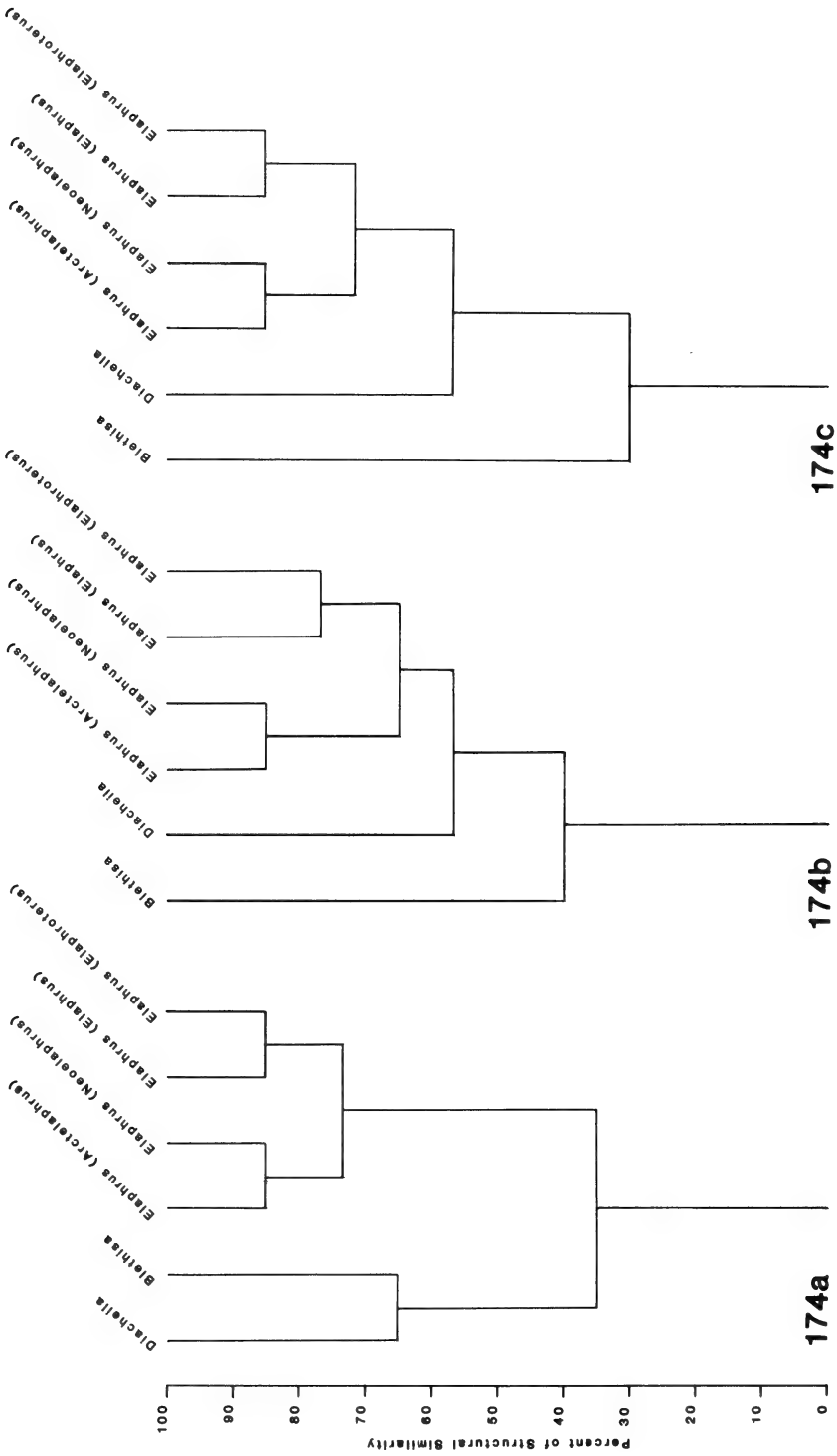


Fig. 174. Phenetic relationships of genera and subgenera of Elaphrini based on a) adults, b) first instar larvae, and c) second instar larvae. See Tables 48 and 49.

## NOTES ON STRUCTURES CORRELATED WITH CRYPTIC COLORATION OF ADULTS OF *ELAPHRUS* WITH THEIR SUBSTRATE

It is striking to observe how adult *Elaphrus* match the substrate on which they live. Adults are cryptically colored, and behave in peculiar ways for carabids to enhance their blending with the environment.

I cannot explain the functional significance of most character states studied. However, many structural features seem correlated with cryptic coloration of adults. Indeed, structural details of dorsal coloration lead quite accurately to the habitat of each species. The structures discussed below are: microsculpture, punctures, elytral pits, mirrors, and color. Most examples are of Nearctic species or Nearctic populations of Holarctic species.

**Microsculpture.** Meshes of microsculpture on the dorsal surface of adults are isodiametric, and sculpticells flat, convex or scale-like. The lack or presence of different types of sculpticells affects the reflected light: lack of sculpticells produces a brilliant surface; presence, especially when sculpticells are convex or scale-like, produces a dull surface. There is a marked correlation between microsculpture of the integument and surface moisture of the substrate on which the beetles live. Meshes are absent over most of intervals on adults of species living on saturated substrates (*E. pyrenoeus*, *E. clairvillei*, *E. olivaceus*, *E. laevigatus*, *E. lecontei*, *E. americanus* and *E. finitimus*), and sculpticells are flat or subconvex on adults of species living on moist but not saturated substrates (*E. uliginosus*, *E. fuliginosus*, *E. cicatricosus*, *E. lindrothi*, *E. ruscarius* and *E. californicus*), and convex or scale-like on those living on moist and firm, or moist and drained substrates (*E. lapponicus*, *E. tuberculatus*, *E. angusticollis*, *E. purpurans* and *E. aureus*).

**Punctures.** Probably the combined effect of punctures is to break the sharp outline of body (Ball, pers. comm.). Because punctures in this genus are brightly metallic, the above effect is probably amplified by the flash effect of reflected light. There is a marked correlation between average density of punctures over the dorsal surface and particle size of the substrate. Adults with punctures five to 15 microns apart are on clay (*E. californicus* and *E. lecontei*), those with punctures ten to 20 microns apart on silt, fine organic mud, or small moss carpet (*E. pyrenoeus*, *E. lindrothi*, *E. olivaceus* and *E. purpurans*), those with punctures 20 to 40 microns apart are on sand and organic mud (*E. uliginosus*, *E. fuliginosus*, *E. marginicollis*, *E. ruscarius*, *E. americanus*, *E. riparius*, *E. tuberculatus*, *E. parviceps* and *E. angusticollis*), and those with punctures 50 to 200 microns apart are on coarse organic substrate such as dead leaves or large moss carpet (*E. lapponicus*, *E. cicatricosus*, *E. clairvillei* and *E. laevigatus*).

**Elytral pits.** Pits are variously impressed. There is a marked correlation between degree of impression of pits and roughness of the substrate. Pits are absent from or barely impressed on adults living on smooth substrates (*E. viridis* and *E. lecontei*), sharply but not deeply impressed on those living on moderately rough substrates (*E. fuliginosus*, *E. lindrothi*, *E. olivaceus*, *E. ruscarius*, *E. californicus*, *E. americanus*, *E. finitimus*, *E. tuberculatus*, *E. purpurans* and *E. angusticollis*), sharply and deeply impressed on those living on rough substrates such as dead leaves (*E. cicatricosus*, *E. clairvillei*, and *E. laevigatus*).

**Elytral mirrors.** Mirrors reflect light with a flash effect. They vary in size and number. Mirrors look like reflection of light from water between substrate particles. There is some correlation between mirror development and substrate moisture. Mirrors are anastomosed with even intervals on adults living on saturated substrates (*E. pyrenoeus*, *E. clairvillei*, *E. olivaceus* and *E. laevigatus*), isolated and numerous on those living on saturated substrates (*E. lecontei*, *E. americanus*, *E. finitimus* and *E. parviceps*), and isolated and few (usually only mirrors of interval 3) on those living on moist substrates (*E. lapponicus*, *E. lindrothi*, *E. cicatricosus*, *E. ruscarius*, *E. californicus* and *E. tuberculatus*). However, the rule does not hold with adults of *Elaphroterus* which have many mirrors and live on moist but not saturated substrates.

**Color.** Color of the dorsal surface is the summation of complex blending of above structures with pigmentation and metallic reflection of the surface. In absence of metallic reflections, the surface is black. Depending on proportion of reflected light, metallic reflections may range from a hue to a brilliant flash. Space between punctures is, in adults of most species less brilliant than punctures. Blending of color from punctures and surrounding surface is similar to our blending of points of primary color on color television monitors. Adults match closely the color of the substrate. In most species, adults of one sample may be represented by two or three discrete color forms. The proportion of these color forms is constant locally, or, in some species, over large territory. The less dominant color forms are also cryptic over part of habitat. Copper-colored or brown specimens are cryptic over brown mud (*E. americanus*, *E. riparius*, and *E. parviceps*), red clay (*E. ruscarius*), red organic mud (*E. lecontei* and *E. americanus*), red or brown mosses (*E. lapponicus* and *E. olivaceus*), and leaf litter (*E. purpurans* and *E. angusticollis angusticollis*). Such association of color forms is probably not random, as observed in large samples of *E. americanus sylvanus* in the subalpine zone in the Cascades where copper-colored adults were markedly more abundant on brown mud than on grass or mosses. However, I do not understand the significance of bicolor adults of *E. californicus* which are less cryptic than common gray-green adults on clay surfaces.

The above discussion clearly stresses the amazing complexity of cryptic coloration in adults of *Elaphrus*. The above hypotheses were tested quite successfully in rediscovering adults of rare species (*E. lindrothi*, *E. viridis*, *E. tuberculatus*, *E. parviceps* and *E. angusticollis*), or in forecasting the habitat of some European species (*E. uliginosus*, *E. pyrenoeus* and *E. cupreus*) before I studied published information.

Cryptic coloration in this genus is an unusual example of trends in a functional complex which could induce systematists into errors about relationships. Indeed, unrelated species pairs living in similar habitats (*E. uliginosus-fuliginosus*, *E. pyrenoeus-olivaceus*, *E. clairvillei-leavigatus*, *E. lindrothi-ruscarius*, *E. ruscarius-riparius*, *E. americanus-riparius*, *E. tuberculatus-angusticollis*) have achieved remarkable parallelisms.

## PHENETICS AND CLADISTICS: LARVAE AND ADULTS

In the following discussion, I establish relationships of the genera and subgenera of Elaphrini using separately the procedures of phenetic and cladistic methods. The purpose is to compare results between both systems and to test each system for congruency of results based on adults and larvae. Therefore four systems of relationships will be presented: two phenetic systems, one for adults and one for larvae; and two cladistic systems, one for adults and one for larvae.

### Phenetic Association

*Numerical methods.*— In this analysis, I used any character with states distributed uniformly within genera and subgenera and excluded characteristics restricted to species level. For each character, I coded the states between zero and one. A coded value of this character was attributed to each taxon. Then the coded value of the character for each taxon was compared to that for each other taxon. If the state for two taxa was similar, I recorded zero; if the values of two states were different, I subtracted one from the other and retained the result as an absolute value. If a character was expressed in a higher taxon as two or more states, the numerical values of these states were added and divided by the number of states in this taxon. This was done for all characters. Finally, the absolute differences of all characters for all possible pairs were summed. The result was divided by the number of characters and expressed as a percent of similarity. The results were then expressed as a phenogram. The index of dissimilarity is expressed as follows:

Index of dissimilarity in percent -  $1/N(\sum_i |X_{ij} - X_{il}|) \times 100$

X - state value of character "i" for taxa "j" and "l"

N - number of characters used.

*Results of numerical classification of adults and larvae.*— Tables 48 and 49 show the coded values and distribution for each character state. Phenograms for adults and larvae are provided in Fig. 174. At the generic level, adults of *Blethisa* and *Diacheila* are more similar (64%) than they are to those of *Elaphrus* (35%) (Fig. 174a). Based on adults, the four subgenera of *Elaphrus* form two groups of two subgenera each. Adults of *Arctelaphrus* are more similar to those of *Neoelaphrus* (85%) than to those of other subgenera. Adults of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (85%) than to those of other subgenera.

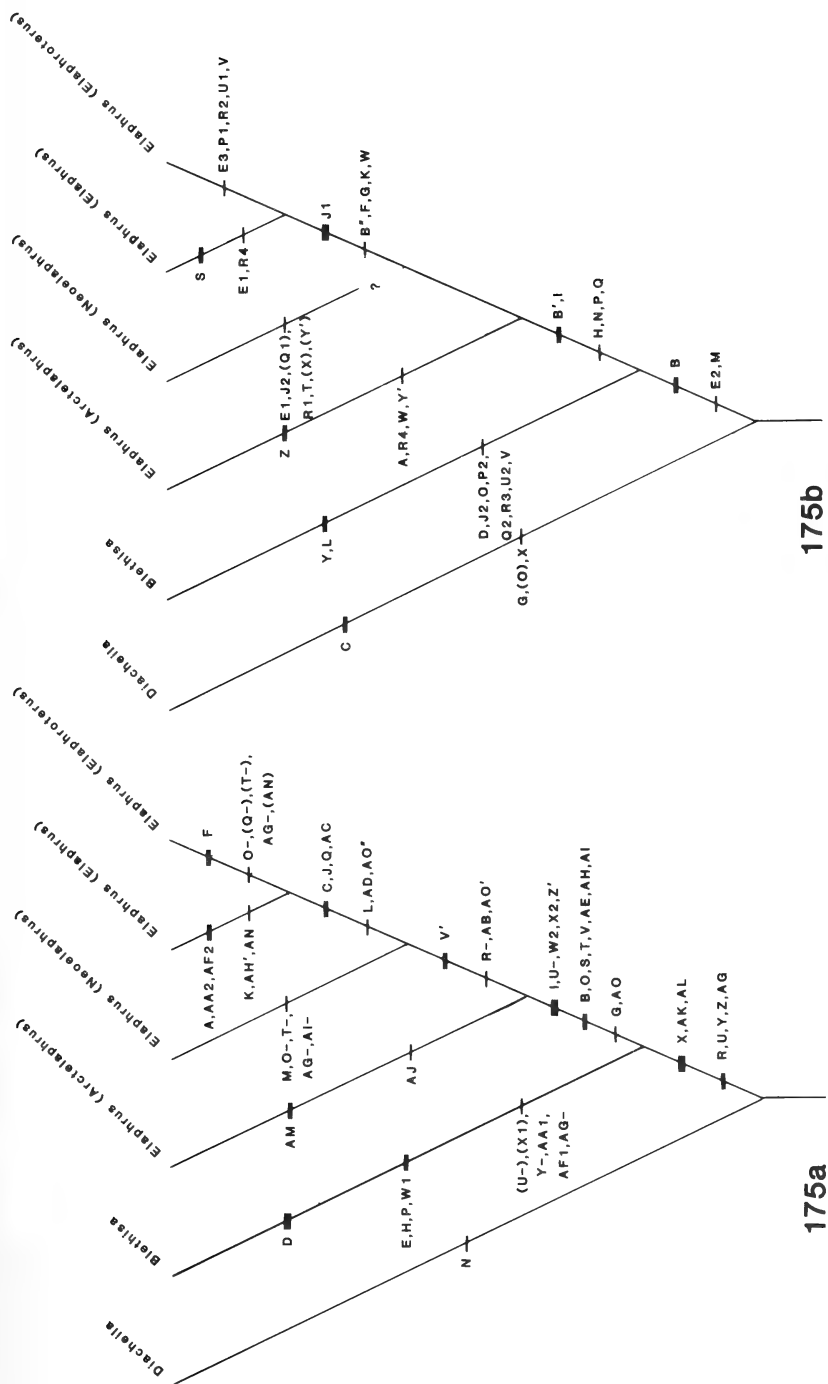


Fig. 175. Reconstructed phylogeny of genera and subgenera of Elaphrini based on a) adults, and b) first, second, and third instar larvae. Capital letters refer to derived states of coded characters (see Tables 50 and 51). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

At the generic level, larvae of *Diacheila* and *Elaphrus* are more similar (57% for first instar larvae, 59% for second instar larvae) than both are to those of *Blethisa* (39% for first instar larvae, 27% for second instar larvae) (Figs. 174b, 174c). Based on larvae, the four subgenera of *Elaphrus* form the same groups of two subgenera each as those based on adults. Larvae of *Arctelaphrus* are more similar to those of *Neoelaphrus* (86% for first instar larvae, 85% for second instar larvae) than to those of other subgenera. Larvae of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (76% of character states of first larvae, 86% of second instar larvae) than to those of other subgenera.

### Phylogenetic Association

*Cladistic methods.*— Hennig (1966), Kavanaugh (1972 and 1978), Whitehead (1972), and Hecht and Edwards (1977) describe the general principles of phylogenetics followed by me. Here, briefly, is the working method I used.

Evolutionary relationships of taxa are determined by recognition of sister taxa. Two or more taxa are likely to share a common ancestor, if they share a derived state of a character (Hennig's (1966) synapomorphic character states). Such group is monophyletic, if it includes all taxa descendant from one common ancestor. A phylogeny is reconstructed step by step, with progressive recognition of sister groups, until all taxa are studied and thus assigned.

*Determination of character states polarity.*— The main problem is to recognize a derived state (Hennig's (1966) apomorphic state) from an ancestral one (Hennig's (1966) plesiomorphic state). Ross (1974), Ball (1975), Hecht and Edwards (1977) summarize the usual approaches. Basically, out-group comparison is used.

*Out-group comparisons.*— If the state of a character, expressed in some members of a taxon studied, occurs among taxa of at least the next higher category, then it is likely an ancestral trait. This is based on the assumption that its extensive distribution is the result of inheritance, not of independent evolution. However, as pointed out by Ekis (1977), a state originally widespread among taxa, following massive extinction, may be sparsely distributed among surviving taxa and the existence of relict taxa should be carefully considered when using this type of evidence.

*Weighting of character states.*— After the polarity of states of one or more characters was decided, I evaluated the weight of each derived state. Some states are of little value since they are likely to have evolved more than once (problems of parallelism and convergence), while other states are so complex or unusual that it is not likely they would have evolved twice in exactly the same structural details. Thus, it is important to select character states of highest weight for phylogenetic reconstruction. Hecht and Edwards (1977) suggested five classes, but I used only three in this work since two of their classes (Hecht and Edwards' class 2 and 3) were not observable or applicable.

In the first class, I included character states showing linear variation (*i.e.*, length of setae and density of punctures) and lost states (*i.e.*, loss of setae, sculpture and pigment). This class, termed "1," is of lowest weight, as reversals and convergent evolution are likely and difficult to detect.

In the second class, I included modified states of simple structures (eg. development of peg-like structure at bases of inner spurs of mid-tibiae of males, and puncture distribution pattern on pronotum.) This class, termed "2", is of moderate weight as reversals and convergences are likely to be detected and their occurrence rare.



In the third class I included new and complex character states (*i.e.*, the complex elytral mirror and pit system in *Elaphrus*, and the complex and integrated stridulatory structures of Elaphrini). This class, termed "3", is of highest weight, as reversals and convergences are most unlikely and would probably be easily detected in an analysis of structural details.

*Phylogenetic reconstruction.*— Sister groups are recognized by shared possession of a derived state of one or more characters. Reconstruction is done in steps. First, groups are assembled with character states of highest weight, then reconstruction with those of moderate weight, and finally with those of lowest weight. However, the entire phylogeny is not completely reconstructed on character states of high weight, but in part on those of lower weight when those of high weight are not available (see Fig. 178). The law of parsimony is not considered except with character states of lowest weight.

*Results of phylogenetic reconstruction.*— Data presented in tables 50 to 59 were used in reconstruction of the phylogenetic diagrams (Fig. 175). In these tables, each character was coded by one letter or a combination of two letters. The derived state was represented by capital symbols. Where three or more states were present, and the two or more derived states arose independently, an integer for a lost state was added to the letter code. If the states were part of a morphocline, I used ("), ('), etc. after the letter code, suggesting a clinal progression. The estimate of weight was expressed as "1" for lowest weight, "2" for moderate weight, and "3" for high weight. Out-group evidence in relation to elaphrine beetles was derived from numerous tribes of carabids: Trachypachini, Metriini, Omophronini, Carabini and Nebriini (assumed to be older lineages); and Trechini, Pterostichini, Agonini, Anisodactylini and Harpalini (assumed to be younger lineages). The justifications in determining polarities of character states are summarized in Table 60.

At the generic level, results of analyses of relationships among adults show that *Elaphrus* shares a common ancestor with *Blethisa*, and that both of these genera share a common ancestor with *Diacheila* (Fig. 175a). At the subgeneric level, *Elaphrus* and *Elaphroterus* share a common ancestor, *Neoelaphrus* shares a common ancestor with the above subgenera, and *Arctelaphrus* shares a common ancestor with the above three subgenera.

At the generic and subgeneric levels, relationships among larvae are similar to those described above for adults (Fig. 175b). However, I failed to show the relationships of *Neoelaphrus* relative to *Arctelaphrus*.

### Comparisons Between Systems of Association

The three genera were paired three ways by the cladograms and the phenograms: one system based on phenetic relationships of adults gave one result, one based on phenetic relationships of larvae gave another, and one based on phylogenetic relationships of adults and larvae gave a third. Therefore, the phenograms, based on adults and larvae are incongruent while the cladograms, based on adults and larvae, are congruent.

The subgenera of *Elaphrus* were associated similarly in phenograms based on adults and larvae and in cladograms based on adults and larvae. However, the relationships of *Neoelaphrus* were different between phenograms and cladograms. In phenograms, *Neoelaphrus* was associated with *Arctelaphrus*; while in cladograms, based on adults, *Neoelaphrus* was the sister group of the *Elaphrus-Elaphroterus* group and *Arctelaphrus* was the sister group of all three subgenera.

The phylogenetic reconstruction based independently on adults and larvae was congruent. However, the cladogram based on larvae was difficult to construct since the evidence of

character state distribution was limited (most previous descriptions of larvae are superficial and hence do not provide data needed for analyses of relationships).

Three genera can be paired only three ways. Numerical analysis produced two systems: *Blethisa* and *Diacheila* most similar for adults and *Diacheila* and *Elaphrus* most similar for larvae. The phylogenetic results based on adults and larvae suggested that *Blethisa* and *Elaphrus* are more closely related.

### Conclusions

*Numerical analysis.*— The incongruent results between adults and larvae in the numerical analysis can be explained by various factors: insufficient data, incorrect numerical technique, incorrect coding of states and appropriateness of concept.

In statistical work one expects to approach the real mean as sample size increases. How many characters are necessary to reach consistent results? In my first analysis of adults (based on one *Diacheila*, two *Blethisa* and 13 *Elaphrus* species), I used 288 characters. The results obtained were consistent at the generic level with classifications based on 88 characters from the thoracic and abdominal pleura and sterna, on 57 characters from the head and the tergites, on 51 characters from the dorsum of the head, the pronotum and the elytra, and on 87 characters from the legs. The only discrepancy was at the subgeneric level of genus *Elaphrus* where *Arctelaphrus* was marginally associated with subgenus *Elaphrus* for leg characters. Therefore, in using 80 to 120 characters in analyses of adults and larvae, I probably had enough characters.

I used the simplest index of similarity. More complex cluster analysis techniques are available. However, the taxa compared are very distinct. Therefore, I do not suspect major differences due to techniques for the association of these genera.

Coding can be criticized since for about 40% of characters used, more than two states were found. However, I obtained similar results using only two-state characters in subanalyses of adults and larvae.

Since I probably used enough characters in these analyses, and satisfactory methods, I feel that incongruent results between genera, based on adults and larvae, suggest that something fundamental is missing in the formulation of taxa association.

Pheneticists measure gaps (percent of similarity) between taxa (OTU's of Sokal and Sneath, 1963). Gaps are caused by two factors: extinction of intermediate taxa, and evolutionary rates. The extinction effect, though important in the classification process, is not important in working out relationships. However, evolutionary rates are probably the most important factor explaining incongruent results.

If species are evolving at similar rates at any stage, the overall changes should be less among recently evolved taxa than among those that are older. Therefore, phenograms based on different stages not only would be congruent but would be a phylogenetic reconstruction. However, evolutionary rates are not only different between species at any stage but these rates are not correlated between stages of the same species.

Since evolutionary rates are not uniform, phenograms, based on different stages, are likely to be incongruent. Phenograms reflect a mixture of effects due to evolutionary rates and recency of descent. Fast-evolving taxa are likely to be singled out (e.g. adult *Elaphrus* or larval *Blethisa*), and slow evolving taxa are likely to be associated (e.g. *Diacheila* and *Blethisa* as adults, and *Diacheila* and *Elaphrus* as larvae). Therefore, the principle of assembling living things based on overall similarity using equally weighted characters is not likely to formulate a

consistent phylogenetic hypothesis. The method used is a measure of distinctness and should not be used for purposes of phylogenetic reconstruction.

*Cladistic analysis.*— The phylogenetic reconstructions, based separately on adults and larvae, are congruent despite different evolutionary rates between species of each stage and uncorrelated evolutionary rates between stages. Some of the evidence shown to unite *Blethisa* to *Elaphrus*, based on adults and larvae, is based on high weight character states. Therefore, I feel that the cladistic reconstruction is the one that is most likely to provide an evolutionary hypothesis.

Table 48. Distribution of characters of adults among genera and subgenera and of coded character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<b>Eye shape:</b>						
small, 0						
typical, 0.5						
prominent, 1.0	0.25	0.5	1	1	1	1
<b>thickness, cornea:</b>						
similar, 0						
thinner ant., 1.0	0	0	0	0	1	1
<b>Head, punctures distribution:</b>						
restricted or absent, 0						
on all of disc, 1.0	1	0	1	1	1	1
<b>Antennae, proportions,</b>						
<i>antennomeres 1:2:</i>						
2x longer, 0						
1.5 to 1.7x longer, 1.0	0	0	1	1	1	1
<b>Mandible, right,</b>						
<i>retinacular basal tooth:</i>						
single, 0						
double, 1.0	0	0	1	1	0	0
<i>retinacular apical tooth:</i>						
near terebral tooth, 0						
distant, 1.0	1	0	1	1	0	0
<b>Maxilla, proportions</b>						
<i>palpomeres 3:4:</i>						
0.67, 0						
0.5, 0.5						
0.3, 1.0	0	0.5	0.5	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<i>lacinia, teeth size:</i>						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
<b>Labium, proportion,</b>						
<i>palpomeres 1:2:</i>						
0.5, 0						
0.7–0.8, 1.0	1	0	1	1	1	1
<b>Mentum, no. setae:</b>						
2, 0						
4, 1.0	0	1	0	0	0	0
<b>Gula, no. setae:</b>						
8, 0						
6, 1.0	0	0	0	0	0	1
<b>Thorax, pronotum,</b>						
<i>no. lateral setae:</i>						
2, 0						
1, 1.0	0	0	1	1	1	1
<i>no. discal impressions:</i>						
0, 0						
1 or more, 1.0	0	0	1	1	1	1
<i>lateral bead:</i>						
complete, 0						
incomplete (sinuation), 0.5						
absent, 1.0	0	0	0.5	0.75	1	1
<i>post. fringe, termination from</i>						
<i>postero-lateral angle:</i>						
before lat. impr., 0						
in lat. impr., 0.5						
at angle, 1.0	0	0.5	0.5	0.75	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<i>fringe, seta shape:</i>						
narrow, 0						
scimitar, 0.5						
wide scimitar, 1.0	0.5	0	0.5	0.5	1	0.5
<i>punctures distr., disc:</i>						
very restricted, 0						
on all of disc, 1.0	1	0	1	1	1	1
<b>Proepisternum, suture</b>						
<i>epist. and epim.:</i>						
distinct, 0						
indistinct, 1.0	0.5	0	0	0	1	1
<i>ridge, epist. and flange:</i>						
complete, 0						
0.5 complete, 0.5						
0.05 complete, 1.0	0.5	0	1	1	1	1
<i>flange size:</i>						
small, 0						
medium, 0.5						
large, 1.0	0	0	0.5	1	1	1
<b>Prosternum, lat. margin</b>						
<i>shape:</i>						
angulate, 0						
sinuate, 1.0	0	0	0	1	0	0
<i>ant. fringe, seta shape:</i>						
narrow, 0						
narrow + scimitar, 0.33						
scimitar, 0.67						
wide scimitar, 1.0	0.33	0	0.67	0.67	1	0.67
<i>disc, setae distribution:</i>						
absent, 0						
intercoxal process, 0.5						
covering disc, 1.0	0	0	1	0.25	1	0.25

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<i>pointed sculpture, cox. cav.</i>						
small points, 0						
large points, 1.0	0	0	1	1	1	1
<b>Scutellum, basal ridge:</b>						
present, 0						
absent, 1.0	1	0	1	1	1	1
<i>punctures:</i>						
present, 0						
absent, 1.0	0	1	0	0	0	0
<b>Mesepisternum,</b>						
<i>anterior submedial ridge:</i>						
distinct, 0						
absent or indistinct, 1.0	0.5	0	1	1	1	1
<b>Mesosternum, lateral ridge:</b>						
distinct, 0						
indistinct, 0.5						
absent, 1.0	1	0	0.5	0.5	1	1
<b>Mesosternum,</b>						
<i>intercoxal process, setae:</i>						
absent, 0						
present, 1.0	0	0	0	0	1	0.5
<b>Metanotum</b>						
<i>size apico-lateral setae:</i>						
large, 0						
small, 1.0	1	0	1	1	1	1
<b>Metepisternum, ant. ridge:</b>						
convex ridge, 0						
ridge distinct, 0.5						
absent, 1.0	0.25	0	0.5	0.5	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<b>Metasternum, ant. acc. setae:</b>						
present, 0						
absent, 1.0	1	1	0	0	0	0
<i>lateral setae:</i>						
present, 0						
absent, 1.0	1	1	0	1	0	0.5
<b>Abdomen, terga</b>						
<i>setae, tergum 1:</i>						
absent, 0						
present, 1.0	0	1	0	0	0	0
<i>ant. submedial ridges, tergum 2:</i>						
absent, 0						
present, 1.0	0	0	1	1	1	1
<i>stridulatory scraper,</i>						
<i>points density:</i>						
20 microns apart, 0						
30–40 microns apart, 1.0	1	0	0	0	0	0
<i>microsculpture, tergum 8:</i>						
absent, 0						
present, 1.0	0.5	0	1	1	1	1
<b>Sterna 3–4,</b>						
<i>medial acc. setae:</i>						
absent, 0						
present, 1.0	0	0.5	1	1	1	1
<i>apical setae, sternum 7:</i>						
2, 0						
4, 1.0	0	1	1	1	1	0.5
<i>puncture distribution:</i>						
sternum 2, 0						
sterna 2–4, 0.5						
sterna 2–6, 1.0	0.5	0	1	1	1	1

(continued on next page)



Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<b>Elytra,</b>						
<i>striae, disc:</i>						
distinct, 0						
indistinct, 0.5						
absent, 1.0	0	0	0.5	0.5	1	1
<i>transverse basal stria:</i>						
complete, 0						
terminated at stria 5, 0.5						
terminated at shoulder, 1.0	0.75	0.25	1	1	1	1
<i>stria 5, base:</i>						
indistinctly impressed, 0						
deeply impressed, 1.0	0.5	0	1	1	1	1
<i>setigerous punctures,</i>						
<i>no. discal rows</i>						
1, 0						
2, 0.5						
3, 1.0	0	0.5	1	1	1	1
<i>size:</i>						
20 microns, 0						
30 microns, 0.5						
40–60 microns, 1.0	0	0	0.5	1	1	1
<i>interval 3:</i>						
entire, 0						
catenate, 0.5						
catenation mirror-like, 1.0	0	0.5	1	1	1	1
<i>pits, ridges:</i>						
absent, 0						
narrow, 0.5						
wide, 1.0	0	0	1	0.75	0	0
<i>punctures:</i>						
absent, 0						
3–25, 0.33						

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
30-50, 0.67						
50 or more, 1.0	0	0	0.33	0.33	1	0.67
<i>intervals 4, 6 and 8,</i>						
<i>punctures:</i>						
present, 0						
absent, 1.0	1	1	0	0	0	0
<i>micropores in punctures:</i>						
few, 0						
regular, 0.5						
common, 1.0	0	0	1	1	0	0.5
<i>elytral articulation</i>						
<i>no. elongate punctures:</i>						
5-7, 0						
2-4, 1.0	0	0	0	0	1	1
<i>elytral epipl., punctures:</i>						
absent, 0						
present, 1.0	1	0	1	1	1	1
<b>Legs, foreleg, coxa,</b>						
<i>punctures:</i>						
absent, 0						
present, 1.0	1	0	1	1	1	1
<i>trochanter, no. setae:</i>						
1, 0						
2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
<i>fermur, no. setae:</i>						
10-25, 0						
30-60, 0.5						
60-80, 1.0	0	0	1	0.5	1	0.5

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<i>tibia, male, no. setae:</i>						
15-27, 0						
30-45, 1.0	0	0	0.5	1	1	0.5
<i>fringe, basal setae:</i>						
4-8, 0						
absent, 1.0	0	0	0	1	1	1
<i>setae no., postero-medial row, male:female:</i>						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
<i>tarsomere, male, no. enlarged:</i>						
4, 0						
3, 1.0	0	0	0	0	1	1
<b>Midleg,</b>						
<i>coxa punctures:</i>						
absent, 0						
present, 1.0	0.5	0	1	1	1	0.5
<i>setae no.:</i>						
1 or 2, 0						
numerous, 1.0	0	0	1	1	1	1
<i>trochanter, setae no.:</i>						
absent, 0						
1 or 2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
<i>femur, setae no.:</i>						
30-45, 0						
80-110, 1.0	0	0	1	0.5	1	0.5
<i>antero-medial row apex:</i>						
expanded, 0						
linear, 1.0	0	0	1	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<b>Hind leg,</b>						
<i>coxa punctures:</i>						
present, 0						
absent, 1.0	0.5	1	0	0	0	0
<i>coxa, setae no.:</i>						
2, 0						
3, 0.33						
3-15, 0.67						
30-40, 1.0	0.33	0	0.67	0.5	1	0.67
<i>trochanter, spinules no.:</i>						
4-6, 0						
10-15, 1.0	0	1	0	0	0	0
<i>femur, setae no.:</i>						
1-4, 0						
5-10, 0.5						
15-30, 1.0	0	0	1	0.5	1	1
<i>tibia, external row:</i>						
absent, 0						
present, 1.0	0	0	1	1	1	1
<i>antero-medial row apex:</i>						
expanded, 0						
linear, 1.0	0	0	1	1	1	1
<b>Male genitalia, median lobe</b>						
<i>baso-dorsal:</i>						
open, 0						
closed, 1.0	1	0	0	0	0	0
<i>stylet, base:</i>						
narrow, 0						
enlarged, 1.0	0	1	1	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
<i>apico-ventral point:</i>						
present, 0						
absent, 1.0	1	0	1	1	1	1
<i>parameres, width,</i>						
<i>right:left:</i>						
0.75, 0						
0.50–0.3, 1.0	0	0	0	0	1	1
<b>Ovipositor, stylus,</b>						
<i>basal sclerite, setae:</i>						
apical 0.67, 0						
apical 0.25, 0.33						
apical 0.1, 0.67						
absent, 1.0	0.5	0	0.67	0.33	1	1
<i>ridge:</i>						
present, 0						
absent, 1.0	0	1	0	0	0	0
<i>apical sclerite, disc,</i>						
<i>setae no.:</i>						
many, 0						
few (4–6), 0.5						
absent, 1.0	0.5	0	0.5	0.5	0.5	1
<i>setae size:</i>						
absent, 0						
fine, 0.5						
stout, 1.0	0.5	0.5	1	1	1	0
<i>apical setae, no. and size,:</i>						
2 small, 0						
2 very small, 0.33						
1 very small, 0.67						
absent, 1.0	0	0	0.33	0.67	1	1

Table 49. Distribution of characters of larvae among genera and subgenera and of coded character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<b>Head, frontale, nasale,</b>							
<i>medial point:</i>							
slightly prominent, 0							
prominent, 0.33							
very prominent, 0.67							
extr. prominent, 1.0	1-3	0	0.33	0.67	0.67	1	1
<i>teeth distribution:</i>							
united, 0							
separated, 0.33							
very separated, 0.67							
extr. separated, 1.0	1-3	0.16	0	0.33	0.33	1	0.67
<i>teeth size:</i>							
absent, 0							
very small, 0.25							
small, 0.5							
large, 0.75							
very large, 1.0	1	0.5	1	0.75	0.37	0.12	0.05
very small, 0							
small, 0.33							
large, 0.67							
very large, 1.0	2-3	0.33	1	0.67	0.67	0	0.33
<i>position seta MMP-E:</i>							
<i>egg-bursters:</i>							
internal, 0							
external, 1.0	1	0	1	1	1	0	0
<i>pore MA-I: seta MMA:</i>							
internal, 0							
parallel, 1.0	1	0	1	1	1	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>seta size, EA-E:</i>							
small, 0							
medium-small, 1.0	1-3	0	1	0	0	0	0.25
<i>EM-P:</i>							
virtually absent, 0							
small, 1.0	1-3	0	1	0	0	0	0
<i>MP:</i>							
virtually absent, 0							
small or larger, 1.0	1-3	0	1	0	0	0	0
<i>Accessory setae size:</i>							
absent, 0							
small, 1.0	2-3	0	1	0	0	0	0
<i>Microsculpture</i>							
<i>antero-medially:</i>							
absent, 0							
present, 1.0	2-3	0	1	0	0	0	0
<i>Parietale shape:</i>							
elongate, 0							
short, 1.0	1-3	1	0	0	0	1	1
<i>occipital suture:</i>							
0.6-1.2 scape 1., 0							
0.2-0.6 scape 1., 1.0	1	0	0	0	0	1	1
<i>position, pore DI-P</i>							
140-160°, 0							
120-130°, 0.5							
90-120°, 1.0	1-3	0	0	0.5	0.5	1	1
<i>seta DI-A:</i>							
post. to post.-lat.							
angle, 0							
level with angle, 1.0	1-3	0	0	0	0	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>seta DMM-P</i>							
level with post.-lat. angle, 0							
anterior, 1.0	1-3	0	0	0	0	1	1
<i>seta VEM-P: setae</i>							
<i>DEP and VEP-P:</i>							
distant, 0							
moderate, 0.5							
close, 1.0	1-3	0.75	0.25	0.5	0.5	0.9	1.0
<i>pore VEM-A: seta VEM-P:</i>							
distant, 0							
close, 1.0	1-3	0	0	1	1	1	1
<i>pore VEP-A: seta VEP-P:</i>							
external, 0							
internal, 1.0	1-3	0	0	1	1	1	1
<i>basic seta size, DI-A:</i>							
small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
<i>DMP-A</i>							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0.5	0.5
very small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
<i>DEP:</i>							
very small, 0							
medium, 0.33							
large, 0.67							
very large, 1.0	1-3	0	1	0.33	0.67	0.33	0.33

(continued on next page)



Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>VMA</i> :							
small, 0							
medium, 0.5							
large, 1.0	1	0	1	0.5	0.5	0	0
small, 0							
medium, 1.0	2-3	0	1	1	1	1	1
<i>VEP-A</i> :							
medium, 0							
very large, 1.0	1-3	0	1	0	0	0	0
<i>VEM-P</i> :							
small, 0							
medium, 0.5							
large, 1.0	1-3	0	1	0.5	0.5	0.5	0.5
<i>VEP-P</i> :							
medium, 0							
large, 0.5							
very large, 1.0	1-3	0	1	0.5	0.5	0	0
<i>no. accessory setae</i> <i>near DMM system</i> :							
0-5, 0							
7-9, 1.0	2	0	1	1	1	0	1
<i>lateral surface</i> :							
3-4, 0							
5-6, 0.5							
7-9, 1.0	2	0	1	0	0	0	0.5
<i>accessory setae size,</i> <i>between DMM-P and</i> <i>DI-A</i> :							
absent, 0							
small, 1.0	2-3	0	1	0	0	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>microsculpture,</i>							
<i>dorso-laterally:</i>							
absent, 0							
lateral, 0.33							
on most, 0.67							
on all, 1.0	1	0	1	0.5	1	0.33	0.5
absent, 0							
lateral, 0.5							
on all, 1.0	2	0	1	1	0	0	0.25
<i>latero-ventrally:</i>							
absent, 0							
latero-basal, 0.5							
lateral, 1.0	1	0	1	1	0.75	0.5	0.75
<i>pointed sculpture,</i>							
<i>dorso-laterally:</i>							
0%, 0							
1–10%, 0.33							
15–30%, 0.67							
70%, 1.0	2	0	0.33	1	0.5	0.33	0.5
<i>latero-ventrally:</i>							
absent, 0							
1–5%, 0.5							
10–30%, 1.0	1	0	0	0	0.75	0	0.75
absent, 0							
3–5%, 1.0	2–3	0	0	0	0.5	0	0.5
<b>Antennae, proportion,</b>							
<i>antennomeres 1:2:</i>							
1.5, 0							
1.0, 1.0	1	1	0	1	1	1	1
<b>Mandibles, base width:</b>							
narrow, 0							
wide, 1.0	1–3	0	0	1	1	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<b>Maxillary stipes,</b>							
<i>proportion,</i>							
<i>ventral view:</i>							
short, 0							
medium, 0.5							
long, 1.0	1-3	0	1	0	0.5	0	0
<i>lateral surface:</i>							
sclerotized, 0							
with unsclerotized							
band, 0.5							
unsclerotized band							
extruded, 1.0	1-3	0.5	0	0.5	0	0.5	1
<i>position,</i>							
<i>interno-basal pore:</i>							
distant, 0							
close, 1.0	1-3	1	0	0	0	1	1
<i>antero-external seta</i>							
<i>vs lacinia:</i>							
posterior, 0							
anterior, 1.0	1-3	1	1	0	0	0	0
<i>seta size,</i>							
<i>antero-internal:</i>							
small, 0							
medium, 1.0	2-3	1	0	0	0	0	0
<i>no. accessory setae,</i>							
<i>postero-external:</i>							
absent, 0							
present, 1.0	2	0	1	0	0	0	0
<i>internal, 0.5, dorsum:</i>							
20-30, 0							
40-50, 1.0	1-3	0	0	0	0	0	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>no. rows in apical 0.3:</i>							
1, 0							
2, 0.5							
3 or more, 1.0	1-3	0	0	0	0	0.5	0.75
<b>Lacinia, shape:</b>							
conical, 0							
suggested, 1.0	1-3	0	0	1	1	1	1
<i>basic setae size,</i>							
extremely small, 0							
small, 1.0	1-3	0.5	0	1	1	1	1
<b>Galea, galeomere 2</b>							
<i>position, internal</i>							
<i>microseta:</i>							
apical 0.6-0.8, 0							
apical 0.6-0.4, 0.5							
apical 0.3-0.1, 1.0	1-3	0.5	0	0.5	0.5	1	1
<i>galeomere 2,</i>							
<i>size basic seta:</i>							
virtually absent, 0							
very small, 0.5							
small or larger, 1.0	1-3	0	0.5	0.5	0.5	1	1
<b>Maxillary palpi,</b>							
<i>proportion,</i>							
<i>palpomeres, 1:2:</i>							
1.5, 0							
1.0, 1.0	1	0	0	0	0	1	1
<b>Labium, ligula size:</b>							
wider, 0							
narrower, 1.0	1-3	0	0	1	1	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>basic seta size,</i> <i>antero-dorsal:</i>							
small or smaller, 0							
medium-small, 1.0	1	0	0	0	0	0	1
<i>very small, 0</i>							
small, 1.0	2-3	0	1	1	1	1	1
<i>no. accessory setae,</i> <i>dorso-laterally:</i>							
2, 0							
5-6, 0.5							
9-15, 1.0	2	0	1	0	0.5	0.5	1
<i>accessory setae size,</i> <i>baso-laterally:</i>							
small, 0							
medium, 1.0	2	0	1	1	1	1	1
<b>Thorax, pronotum,</b> <i>basic seta size, MI:</i>							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0	1	0	0.5
<i>ME-I:</i>							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0	1	1	0.5
<i>PII-P:</i>							
very small, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0.5	1	0	0.5

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>no. accessory setae</i>							
<i>disc:</i>							
5, 0							
15–20, 0.33							
25–50, 0.67							
90 or more, 1.0	2	0	1	0.33	0.33	0.33	0.67
<i>epipleuron:</i>							
1, 0							
2, 0.33							
3, 0.67							
12–14, 1.0	2	0	1	0.1	0.4	0.1	0.2
<i>accessory setae size,</i>							
<i>posterior row:</i>							
absent, 0							
small, 1.0	2–3	0	1	1	1	1	1
<i>epipleuron:</i>							
absent, 0							
very small, 0.33							
medium-small, 0.67							
medium-large, 1.0	2	0	1	0.33	0.67	0.5	0.5
<i>microsculpture, disc:</i>							
absent, 0							
5–20%, 0.33							
60%, 0.67							
100%, 1.0	1	0	0.33	0.67	0.16	1	0.67
absent, 0							
10–75%, 0.5							
100%, 1.0	2	0	0.5	1	0.25	1	0.5
<i>pointed sculpture, disc:</i>							
absent, 0							
3–5%, 1.0	1	0	0.5	0	0	1	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>episternum</i> , <i>size basic setae</i> :							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0	0.5
<i>accessory setae</i> :							
small, 0							
medium, 1.0	2	0	1	0	0	0	0
<i>epimeron</i> , <i>size basic setae</i> :							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0.5	0.5	0.5	0.5
<i>no. accessory setae</i> :							
1, 0							
5-7, 1.0	2	0	1	0	0	0	0
<i>sternite</i> , <i>no. accessory setae</i> :							
2, 0							
10, 1.0	2	0	1	0	0	0	0
<b>Mesonotum</b> , <i>size basic setae</i> ,							
<i>PIM-I and PIE-A</i> :							
medium, 0							
large, 1.0	1-3	1	1	1	1	0	0
<i>PII-P</i>							
absent, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0.5	1	0.5	0.5

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>no. accessory setae;</i>							
<i>disc:</i>							
8, 0							
15-20, 0.33							
40, 0.67							
60-80, 1.0	2	0	1	0.33	0.33	0	0.5
<i>epipleuron:</i>							
1-2, 0							
4-5, 0.5							
7-13, 1.0	2	0	1	0	0.25	0	0.25
<i>accessory setae size,</i>							
<i>posterior row:</i>							
absent, 0							
small, 1.0	2	0	1	1	1	0.75	0.5
<i>microsculpture, disc:</i>							
10-50%, 0							
60-70%, 1.0	1	0	0	1	0	1	1
0-5%, 0							
20-40%, 0.5							
90-100%, 1.0	2	0	0.5	1	0.5	1	1
<i>pointed sculpture,</i>							
<i>disc laterally:</i>							
5-15%, 0							
25-35%, 1.0	1	0	0	0	0	1	0.5
<i>anterior band,</i>							
absent, 0							
30-50%, 0.5							
100%, 1.0	2	0	0.25	0	0	0.5	1
<i>posterior band</i>							
absent, 0							
30-50%, 0.5							
100%, 1.0	1-3	0	0	0	0.25	0.5	1

(continued on next page)



Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>anterior pleurite,</i> <i>basic seta size:</i> very small, 0 medium, 1.0	2	0	1	0	0	0	0
<i>epipleuron,</i> <i>basic seta size:</i> small, 0 medium, 0.5 very large, 1.0	1	0.5	1	0.5	0.5	0	0.5
medium-small, 0 large, 1.0	2-3	0	1	0	0.5	0	0
<i>no. accessory setae:</i> 1-3, 0 9-16, 1.0	2	0	1	0	0.5	0	0
<i>accessory setae size:</i> absent, 0 very small, 0.5 medium-small, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
<i>microsculpture:</i> absent, 0 single-pointed, 1.0	2-3	0	0	0	0	0	1
<i>episternum,</i> <i>no. accessory setae:</i> 1, 0 3-6, 1.0	2	0	1	0	0	0	0
<i>epimeron,</i> <i>no. accessory setae:</i> 1, 0 4-10, 1.0	2	0	1	0.5	0	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>anterior sternite,</i>							
<i>basic setae size:</i>							
absent, 0							
very small, 1.0	1	0	1	1	1	1	1
absent, 0							
small, 0.5							
medium, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
<i>no. accessory setae:</i>							
0, 0							
2-3, 1.0	2	0	1	0	0	0	0
<i>sternite,</i>							
<i>basic setae size:</i>							
small, 0							
medium, 1.0	1	0	1	1	1	0	1
medium, 1.0	2	0	1	0	0	0	0
<i>no. accessory setae:</i>							
0, 0							
3, 1.0	2	0	1	0	0	0	0
<b>Abdomen, terga,</b>							
<i>basic setae size,</i>							
<i>AII and AIM (1-8):</i>							
medium, 0							
large, 1.0	1	0	1	0	0	0	0
small, 0							
medium, 1.0	2-3	0	1	1	1	1	1
<i>AIM (1-8):</i>							
similar on all, 0							
abruptly smaller, 1.0	1-3	0	0	0	0	1	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>PII-P (1-8):</i> very small, 0 small, 0.5 medium, 1.0	1-3	0	1	0	0	0	0.5
<i>MPP-E (9):</i> absent, 0 small, 1.0	2-3	0	1	1	0.5	0.5	1
<i>AM-P (10):</i> very small, 0 small, 0.5 large, 1.0	1	0.5	1	0.5	0.5	0	0.5
small, 0 medium, 0.5 large, 1.0	2-3	0	1	0.5	0.75	0.5	0.5
<i>PI-P (10):</i> small, 0 medium, 0.5 large, 1.0	2-3	0	1	0.5	1	0.5	0.5
<i>no. accessory setae,</i> <i>disc (1-8):</i> 7-10, 0 15-20, 0.33 25-30, 0.67 40, 1.0	2	0	1	0.33	0.5	0	0.5
<i>urogomphus (9):</i> 7, 0 15-25, 1.0	2	0	1	0	0.5	0	0
<i>disc (10):</i> absent, 0 2-3 major, 1.0	2	0	1	0	0.5	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
absent, 0							
1 minor, 0.1							
4-5 minor, 0.2							
20 minor, 1.0	2	0.2	1	0.1	0.15	0	0.05
<i>position, acc. setae,</i>							
<i>antero-lateral major:</i>							
lateral, 0							
antero-dorsal, 1.0	2-3	0	0	0	0	1	1
<i>microsculpture, type,</i>							
<i>anterior 0.5, disc:</i>							
single-pointed, 0							
multi-pointed, 1.0	1	1	0	1	1	1	1
<i>disc (2-4):</i>							
absent, 0							
single-pointed, 0.5							
multi-pointed, 1.0	2-3	0	0.25	0	0.5	0.5	1
<i>urogomphus (9):</i>							
scale-like, 0							
single-pointed, 1.0	2-3	0	1	0	1	0	0
<i>pointed sculpture,</i>							
<i>disc (4-5):</i>							
5%, 0							
100%, 1.0	2	0	1	1	0.5	1	1
<i>terga no., restricted:</i>							
1-3, 0							
1-7, 1.0	2	1	0	0	0.5	0	0
<i>anterior band (1-8):</i>							
0-5%, 0							
100%, 1.0	1	0	0	0	0	0	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
0%, 0							
50%, 0.5							
100%, 1.0	2	0	0.5	0	0	1	1
<i>anterior band (9):</i>							
0%, 0							
10%, 0.5							
100%, 1.0	2	0	0.5	0	0.25	1	1
<i>epipleuron, shape (1-8):</i>							
entire, 0							
divided, 1.0	2-3	0	1	0	0	0	0
<i>basic seta size,</i>							
<i>anterior seta:</i>							
medium, 0							
large, 1.0	1-3	0	1	0	0	0	0
<i>anterior seta (1-8):</i>							
similar on all, 0							
abruptly changed, 1.0	1-3	1	0	1	1	1	1
<i>anterior seta (9):</i>							
small, 0							
medium, 1.0	1-3	0	1	0	1	0	0.5
<i>no. accessory setae:</i>							
3-4, 0							
8, 0.33							
12-15, 0.67							
30, 1.0	2	0	0.67	0.33	0.67	0.33	0.5
<i>hypopleuron, (1-8):</i>							
<i>no. accessory setae:</i>							
4-6, 0							
12-16, 0.5							
20, 1.0	2	0	1	0	0.5	0	0.75

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>accessory setae size,</i> <i>major setae:</i> medium, 0 large, 1.0	2	0	0	1	1	1	1
<i>minor setae:</i> very small, 0 small, 0.5 medium, 1.0	2	0	1	0.5	1	0.5	0.5
<i>sternite,</i> <i>no. accessory setae</i> (1): 2-6, 0 8-16, 1.0	2	0	1	0	0	0	0
(2-7): 8-20, 0 30-40, 1.0	2	0	1	0	0	0	0
(8): 8-15, 0 20-25, 0.5 40-45, 1.0	2	0	1	0	0.25	0	0
(9): absent, 0 4-6, 0.5 16-26, 1.0	2	0	1	0	0	0	0.5
(10), <i>major setae:</i> 2, 0 3, 0.5 5, 1.0	2	0	1	0.5	0.5	0	0
(10), <i>minor setae:</i> 3-4, 0 6, 0.5 14, 1.0	2	0.5	1	0	0.25	0	0.5

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
<i>microsculpture:</i> absent, 0 15% of (9), 0.5 30% of (9), 1.0	1	0	1	1	0.5	1	1
(2-9): single-pointed, 0 s. and m. pointed, 0.5 multi-pointed, 1.0	2-3	0.5	0.5	1	1	0	0
<i>external poststernite,</i> <i>no. accessory setae,</i> (1): 1, 0 2-4, 0.5 7, 1.0	2	0	1	0.5	0.5	0.5	0.5
(2-7): 3-4, 0 7-10, 1.0	2	0	1	0	0.5	0	0
<i>internal poststernite,</i> <i>basic int. seta size,</i> (1-8): very small, 0 small, 0.5 medium-small, 1.0	1-3	0	1	0	0	0	0.5
(9): very small, 0 small, 0.5 medium-small, 1.0	1-3	0	1	0	0	0	0.5
<i>no. accessory setae,</i> (1): 0-2, 0 6, 1.0	2	0	1	0	0	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Stage	D	B	A	N	E	Et
(2-7):							
1-2, 0							
3-4, 1.0	2	0	1	0	0.5	0	0



Table 50. Distribution of selected characters of adults among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Weight	D	B	A	N	E	Et
<b>Clypeus, setae:</b>							
2, a							
4, A	2	a	a	a	a	A	a
<b>Eye, convexity:</b>							
typical, b							
very prominent, B	2	b	b	B	B	B	B
<b>Cornea, thickness:</b>							
thinner ant., c							
similar, C	2	c	c	c	c	C	C
<b>Frons, lateral sulci:</b>							
straight, d							
octagonal, D	3	d	D	d	d	d	d
<b>Mentum, no. setae:</b>							
2, e							
4, E	2	e	E	e	e	e	e
<b>Submentum, no. setae:</b>							
8, f							
6, F	2	f	f	f	f	f	F
<b>Pronotum, lat. setae:</b>							
2, g							
1 or 0, G	1	g	g	G	G	G	G
<b>lat. margin:</b>							
narrow, h							
explanate, H	2	h	H	h	h	h	h
<b>no. disc impr.:</b>							
absent, i							
1 or more, I	3	i	i	I	I	I	I

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Weight	D	B	A	N	E	Et
<i>post fringe:</i>							
ended bef. hind angle, j							
ended at hind angle, J	2	j	j	j	j	J	J
<i>shape fringe setae:</i>							
narrow, scimitar, k							
wide, scimitar, K	1	k	k	k	k	K	K
<b>Epist.:</b> <i>epim. suture:</i>							
distinct, l							
indistinct, L	1	l	l	l	l	L	L
<b>Prosternum, lat. marg.:</b>							
sinuate, m							
angulate, M	1	m	m	m	M	m	m
<i>ant. fringe:</i>							
1 type setae, n							
2 types setae, N	1	N	n	n	n	n	n
<i>discal setae:</i>							
present, O	2						
absent, O- and o	1	o	o	O	O-	O	O-
<b>Scutellum, b. ridge:</b>							
absent, p							
present, P	2	p	P	p	p	p	p
<b>Mesosternum, coxal setae:</b>							
absent, q or Q-	1						
present, Q	2	q	q	q	q	Q	Q,Q-
<i>lat. ridge:</i>							
absent, r or R-	1						
present, R	2	r	R	R	R-,R	R-	R-

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Weight	D	B	A	N	E	Et
<b>Metasternum, antero-medial</b>							
<i>setae:</i>							
absent, s							
present, S	2	s	s	S	S	S	S
<i>lat. setae:</i>							
present, T	2						
absent, t and T-	1	t	t	T	T-	T	T, T-
<b>Abdominal sterna 3-4</b>							
<i>accessory setae:</i>							
absent, u or U-	1						
present in males, U	2						
on m. and f., U'	3	u	U, U-	U'	U'	U'	U'
<b>Elytra</b>							
<i>setigerous punct.:</i>							
15-20 microns, V							
30 microns, V	2						
40-50 microns, V'	2	v	V'	V	V'	V'	V'
<i>striae, disc:</i>							
present, w							
7-8 irregular, W1	2						
absent, W2	3	w	W1	W2	W2	W2	W2
<i>striae 2 and 3:</i>							
entire, x							
catenate ant. and post. to setigerous puncture, X	3						
catenate ant. to setigerous punct., X1	1						
circle around set. punct. larger X2	3	x	X, X1	X2	X2	X2	X2

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Weight	D	B	A	N	E	Et
<i>interval, no. rows</i>							
<i>setigerous punct.:</i>							
3, y							
3, 5 and 7, Y	2						
3, 5, Y-	1	y	Y-	Y	Y	Y	Y
<i>intervals, 4, 6 and 8:</i>							
<i>entire, z</i>							
catenate, Z	2						
cat. mirror-like, Z1,Z2	3	z	Z-Z1	Z2	Z2	Z2	Z2
<b>Foreleg, trochanter:</b>							
1 seta, AA1	1						
2 setae, aa							
3 setae, AA2	2	aa	AA1	aa	aa	AA2	aa
<i>tibia, post. fringe:</i>							
4-8 setae, ab							
0 or 1 seta, AB	1	ab	ab	ab	AB	AB	AB
<i>no. setae postero-medial</i>							
<i>row m. vs. f.:</i>							
similar, ac							
very dissimilar, AC	2	ac	ac	ac	AC	AC	AC
<i>no. enlarged male</i>							
<i>tarsomeres:</i>							
4, ad							
3, AD	1	ad	ad	ad	ad	AD	AD
<b>Midleg, coxa no. setae:</b>							
1 or 2, ae							
numerous, AE	2	ae	ae	AE	AE	AE	AE
<i>trochanter no. setae:</i>							
0, AF1	1						
1 or 2, af							
3, AF2	2	af	af-AF1	af	af	AF2	af

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	D	TAXA AND DISTRIBUTION OF CHARACTER STATES				
			B	A	N	E	Et
<i>tibia, male apico-internal point:</i>							
absent, ag or AG-	1						
present, AG	2						
AG*=AG,AG-		ag	AG*	AG	AG*	AG	AG*
<b>Hind leg, coxa</b>							
<i>extension, setae:</i>							
absent, ah							
inner 0.5, AH	2						
on all, AH'	1	ah	ah,AH	AH	AH	AH'	AH
<i>femur, no. setae:</i>							
5 or less, ai							
20 or more, AI	2						
6 or 12, AI-	1	ai	ai	AI	AI-	AI	AI
<b>Microsculpture, dorsum:</b>							
alveolae flat to subconvex, aj							
alveolae convex, AJ	1	aj	aj	AJ	aj	aj	aj
<b>Male genitalia, median lobe,</b>							
<i>baso-dorsal surface:</i>							
closed, ak							
open, AK	3	ak	AK	AK	AK	AK	AK
<i>med. lobe, stylet post.:</i>							
narrow, al							
enlarged, AL	3	al	AL	AL	AL	AL	AL
<i>dorsum, right apex:</i>							
smooth, am							
lat. point, AM	2	am	am	AM	am	am	am

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES						
	Weight	D	B	A	N	E	Et
<i>parameres, seta size:</i>							
short, an							
long, AN	1	an	an	an	an	an,AN	an-AN
<b>Ovipositor, stylus, apical</b>							
<i>sclerite setae:</i>							
2 small, ao							
2 very small, AO	1						
1 very small, AO'	1						
0, AO''	1	ao	ao	ao	AO'	AO''	AO''

Table 51. Distribution of selected characters of larvae among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES						
Stage	Weight	D	B	A	N	E	Et	
<b>Head, color:</b>								
yellow and brown, a								
orange, A	1-3	1	a	a	A	a	a	a
<b>Nasale</b>								
<i>med. projection:</i>								
short, b								
long, B		2						
very long, B'		2						
extr. long, B"	1-3	1	b	B	B'	B'	B"	B"
<i>projection, apex:</i>								
single-pointed, c								
3-pointed, C	1-2	2	C	c	c	c	c	c
<i>teeth, position:</i>								
lateral, d								
medial, D	1-2	1	d	D	d	d	d	d
<i>teeth size:</i>								
small, e or E3		1						
very small to absent E1		1						
large, E2	2	1	e	E2	E2	E2,E1	E1	E3
<b>Parietale</b>								
<i>occipital suture:</i>								
1.0-1.2								
scape length, f								
0.2-0.6								
scape length, F	2-3	1	f	f	f	f	F	F

(continued on next page)

Table 51 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES						
Stage	Weight	D	B	A	N	E	Et	
<i>length:</i>								
long head, g								
short head, G	1-3	1	G	g	g	g	G	G
<i>pore VEP-A,</i>								
<i>position:</i>								
int. to VEP-P, h								
ext. to VEP-P, H	1-3	1	h	h	H	H	H	H
<b>Mandible, base width:</b>								
narrow, i								
wide, I	1-3	2	i	i	I	I	I	I
<b>Stipes, ext. surface:</b>								
sclerotized, J2								
narrow unsc.								
band, j								
unsc. band +								
bump, J1	2-3	3	j	J2	j	J2	J1	J1
<i>int. brush,</i>								
<i>no. rows:</i>								
1 apical 0.33, k								
2-3, K	1-3	1	k	k	k	k	K	K
<i>acc. setae, external</i>								
<i>surface:</i>								
absent, l								
present, L	2-3	2	l	L	l	l	l	l
<b>Galeomere 1, seta:</b>								
virtually absent, m								
v. small M	1-3	1	m	M	M	M	M	M
<b>Lacinia, shape:</b>								
coniform, n								
suggested, N	1-3	1	n	n	N	N	N	N

(continued on next page)



Table 51 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES						
Stage	Weight	D	B	A	N	E	Et	
<i>seta size:</i>								
small, o								
extra. small, O	1-3	1	o, O	O	o	o	o	o
<b>Pronotum, disc,</b>								
<i>accessory setae:</i>								
4-5, p								
10-20, P		1						
30-40, P1		1						
90 or more, P2	2	1	p	P2	P	P	P	P1
<b>Pronotal epipleuron</b>								
<i>accessory setae:</i>								
O, q								
2-3, Q		1						
5-7, Q1		1						
12-14, Q2	2	1	q	Q2	Q	Q, Q1	Q	Q
<b>Mesonotum, disc,</b>								
<i>no. acc. setae:</i>								
8-10, r or R4		1						
12-15, R1		1						
20-40, R2		1						
60-70, R3	2	1-2	r	R3	R4	R1	R4	R2
<b>Abdomen, terga 1-8</b>								
<i>seta AIM size:</i>								
similar on 1-8, s								
abruptly smaller, S	1-2	2	s	s	s	s	S	s
<b>epipleuron, size</b>								
<i>anterior seta:</i>								
small, t								
medium-small, T	1-3	1	t	t	t	T	t	t

(continued on next page)

Table 51 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES						
Stage	Weight	D	B	A	N	E	Et	
<i>sternites 2-7,</i>								
<i>no. acc. setae:</i>								
14-25, u		1						
30-40, U1		1						
90-150, U2	3	1	u	U2	u	u	u	U1
<i>internal</i>								
<i>poststernite,</i>								
<i>int. seta size 1-8:</i>								
very small, v								
small, V	1-3	1	v	V	v	v	v	V
<i>microsculpture,</i>								
<i>extension, nota:</i>								
restricted or								
absent, w								
widespread, W	1-3	1	w	w	W	w	W	W
<i>pointed sculpture,</i>								
<i>terga 4-5:</i>								
on all of disc, x								
5% of disc, X	2	1	X	x	x	x,X	x	x
<i>urogomphus:</i>								
single-pointed, y		2						
scale-like, Y		1						
absent, Y'	1-3	1	y	Y	Y'	y,Y'	y	y
<i>sternite 9:</i>								
no meshes, z								
meshes distinct, Z	3	2	z	z	Z	z	z	z

Table 52. Distribution of selected characters of adults among groups of subgenus *Neoelaphrus* and evolutionary classification of the character states. (Taxa abbreviated 'u' for *uliginosus*, 'f' for *fuliginosus* and 'c' for *cupreus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	u	f	c
<b>Eye, cornea thickness:</b>				
40–60 Microns, a				
100 microns, A	1	a	A	a
<b>Pronotum, lateral bead:</b>				
thick, 20–30 microns, b				
thin, 10–15 microns, B1	1			
absent, B2	1	b	b, B2	B1
<b>lateral margin, lat. view:</b>				
straight, c				
sinuate at middle, C	2	C	c	c
<b>termination of post. fringe:</b>				
40–120 microns from hind angle, d				
150–200 microns, D	1			
200–250 microns, D'	1	d	D, D'	D'
<b>disc, antero-submedial impr.:</b>				
absent, e				
present, E	1	E, e	e	e
<b>Abdomen, sterna 5 and 6</b>				
<b>accessory setae:</b>				
present, f				
absent, F or F–	1	f	F	f, F–
<b>Foreleg, males, base post. spur:</b>				
without large point, g				
with large point, G	1	g	G	g
<b>Punctures, surrounding surface of pleura:</b>				
narrowly or not depressed, h				
widely depressed (80 microns), H	2	h	H	h

(continued on next page)

Table 52 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	u	f	c
<i>size, pleura:</i>				
30–45 microns, i				
20–30 microns, I	1	i	i	I
<b>Male genitalia, apex median lobe</b>				
<i>lateral view:</i>				
narrow, j				
wide, J1	1			
very wide, J2	1	j	J1	J2,j

Table 53. Distribution of selected characters of adults among species of *uliginosus* group and evolutionary classification of the character states. (Taxa abbreviated 's' for *splendidus*, 'J' for *japonicus*, 'u' for *uliginosus*, 'p' for *pyrenaicus*.)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES			
		s	j	u	P
<b>Dorsum, color:</b>					
Green, k					
brilliant green, K	1				
brown copper, K1	1	K	K1	k	K1
<b>Color of elytral pits:</b>					
purple metallic, l					
green metallic, L	1	L	l	l	l
<b>Pronotum, antero-lateral impr.:</b>					
absent, m					
present, M	1	m	M	M	M
<b>Elytra, sutural mirrors:</b>					
flat and distinct, n					
convex and distinct, N1					
flat and indistinct, N2	1	N1	n	n	N2
<b>no. rows mirrors:</b>					
2, o					
4, O	1	O	o	o	o
<b>Hind leg, coxa, no. setae:</b>					
3–7, p					
8–15, P	1	P	p	p	p
<b>Punctures, density</b>					
<i>pronotum:elytra:</i>					
similar, q					
dissimilar, Q	2	Q	q	q	q
<b>intervals 4, 6 and 8</b>					
30–40 microns apart, r					
100–150 microns apart, R1	1	r	R1	r	r

(continued on next page)

Table 53 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES				
	Weight	s	j	u	P
<b>Microsculpture meshes:</b>					
widespread, s					
very restricted, S	1	S	s	s	S
<b>Male genitalia,</b>					
<i>apex median lobe,</i>					
<i>dorsal view:</i>					
narrow + straight					
(20–30 microns), t					
wide + twisted					
(60–65 microns), T1	1	t	t	T1	T1
<i>lateral view:</i>					
narrows, j					
enlarged ventrally, J3	1	j	J3	j	j

Table 54. Distribution of selected characters of adults among species of the *fuliginosus* group and evolutionary classification of the character states. (Taxa abbreviated 'f' for *fuliginosus*, 'l' for *lindrothi*, 'c' for *cicatricosus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	f	l	c
<b>Color, dorsal:</b>				
green, k				
very dark copper, K2	1			
silvery-brass, K3	1	k	K3	K2
<b>Color, tarsomeres:</b>				
purple, u				
green, U	1	U	u	u
<b>Pronotum, lateral bead:</b>				
thick (20–30 microns), b				
absent, B2	1	b	B2	B2
<b>termination of post. fringe:</b>				
150–200 microns to hind angle, D				
200–250 microns to hind angle, D'	1	D	D'	D'
<b>Abdomen, sternum 7, males, accessory setae:</b>				
present, v				
absent, V	1	v	V	V
<b>Elytra, sutural mirrors:</b>				
distinct and flat, n				
indistinct and flat, N2	1	n	N2	n
<b>Foreleg, trochanter, setae:</b>				
2, w				
1, W	1	w	w	W
<b>Punctures, density, intervals 4, 6 and 8:</b>				
30–40 microns, r				
10–200 microns, R2	1			
10–30 microns, R3	1	r	R3	R2

Table 55. Distribution of selected characters of adults among species of the *cupreus* group and evolutionary classification of the character states. (Taxa abbreviated as 's' for *sibiricus*, 'cu' for *cupreus*, 'cl' for *clairvillei*, 'o' for *olivaceus*, and 'l' for *laevigatus*.)

CHARACTERS AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Weight	s	cu	cl	o	l
<b>Color, <i>dorsum</i>:</b>						
green, k						
dark copper, K4						
black, K5	1	k	K4	k	k	K5
<b>Pronotum, <i>discal impr.</i>:</b>						
2, x						
1, X	1	x	x	X	x	X
<b>Prosternum, <i>intercoxal process</i>:</b>						
with setae, y						
without setae, Y	1	y	y	y	Y	Y
<b>Abdomen, <i>sterna 5 and 6</i>:</b>						
with accessory setae, f						
without, F-	1	f	f	f	F-	f
<b>Abdomen, <i>sternum 7, males</i>:</b>						
with accessory setae, v						
without, V	1	v	v	v	V	v
<b>Elytra, <i>mirrors</i>:</b>						
distinct, n						
indistinct, N2	1	n	n	N2	N2	N2
<b><i>pits, lateral ridges</i>:</b>						
separated, z						
fused, Z	1	z	z	Z	Z	Z
<b><i>setigerous punctures</i>:</b>						
distinct, aa						
indistinct, AA	1	aa	aa	aa	aa	AA
<b>Midleg, <i>tibia</i>, <i>apico-internal points</i>:</b>						
present, ab						
absent, AB	1	ab	ab	ab	AB	AB

(continued on next page)



Table 55 (continued)

CHARACTERS AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Weight	s	cu	cl	o	l
<b>Punctures, size, dorsum:</b>						
20–30 microns, ac						
10–20 microns, AC	1	ac	ac	ac	AC	AC
<b>density, pleuron:</b>						
30–40 microns apart, ad						
10–20 microns apart, AD	1	ad	ad	ad	AD	AD
<b>density, intervals 4, 6 and 8:</b>						
30–40 microns apart, r						
10–20 microns apart, R4	1					
10–200 microns apart, R5	1					
200 microns or more, R6	1					
50–100 microns apart, R7	1	r	R7	R5	R4	R6
<b>density, metasternum, antero-medially:</b>						
50–100 microns apart, ae						
20 microns apart, AE	1	ae	ae	ae	AE	ae
<b>no. in pits:</b>						
8–15, af						
3–5, AF	1	af	af	af	af	AF
<b>Microsculpture meshes, dorsum:</b>						
expanded, s						
very restricted, S	2	s	s	S	S	S
<b>Male genitalia, apex med. lobe, dorsal view:</b>						
thin and straight (20–30 microns), t						
thick (50 microns) + twisted, T2	1	t	t	T2	t	t

(continued on next page)

Table 55 (continued)

CHARACTERS AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Weight	s	cu	cl	o	l
<i>length of apex in dorsal view:</i>						
moderate, ag						
long, AG1	2					
short, AG2	2	AG1	AG1	ag	AG2	AG2
<i>lateral view:</i>						
narrow, j						
wide, J2	1	J2	J2	j	j	j

Table 56. Distribution of selected characters of larvae among species of subgenus *Neolaphrus* and evolutionary classification of the character states and their weight (taxa abbreviated: 'fu' = *fuliginosus*, 'li' = *lindrothi*, 'ci' = *cicatricosus*, 'cu' = *cupreus*, 'cl' = *clairvillei*, 'ol' = *olivaceus*, 'la' = *laevigatus*).

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES									
	Stage	Weight	fu	li	ci	cu	cl	ol	la	
<b>Nasale;</b> toothed, ah smooth, AH	1-3	1	ah	AH	AH	ah	ah	ah	ah	
<b>Parietale, color:</b> 75% dark, ai 10-20% dark, AI	2-3	1	AI	AI	AI	ai	ai	ai	ai	
<b>Epicranial suture:</b> long, aj short, AJ	1-3	1	AJ	AJ	AJ	aj	aj	aj	aj	
<b>microsculpture dorsal extension:</b> 15-25%, ak 5-10%, AK1 0-1%, AK2 50-80%, AK3	1	1	AK1	AK1	AK2	ak	ak	AK3	AK3	

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES							
	Stage	Weight	fu	li	ci	cu	cl	ol	la
<b>Pronotum, no. acc. setae:</b>									
25–30, al									
70–90, AL1		1							
90–120, AL2	3	1	AL1	AL2	AL2	al	al	al	al
<b>Metanotum, pointed sculpture, near suture:</b>									
present and narrow, am									
absent, AM1		1							
present and wide, AM2	2–3	1	AM1	am	AM1	am	am	am	AM2
<b>pointed sculpture, lateral:</b>									
present, an									
absent, AN	2–3	1	an	an	AN	an	an	AN	AN
<b>no. acc. setae:</b>									
15–25, ao									
35–45, AO	3	1	ao	AO	AO	ao	ao	ao	ao

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES								
		Stage	Weight	fu	li	ci	cu	cl	ol	la
<i>epipleuron</i> , no. acc. setae:										
0-3, ap		2-3	1	ap	ap	AP	ap	ap	ap	ap
5-10, AP										
<b>Abdomen, terga 1-8, no. acc. setae:</b>										
25-35, aq										
60-80, AQ1			1							
90-110, AQ2			1							
125-150 AQ3		3	1	AQ1	AQ2	AQ3	aq	aq	aq	aq
<b>Urogomphus, no. acc. setae:</b>										
7, ar										
9-14, AR			1							
20-40, AR'		2-3	1	AR	AR	AR'	ar	ar	ar	ar
<i>terga 5-8, pointed sculpture:</i>										
over, as										
restricted, AS		2-3	1	as	as	AS	as	as	as	as

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES								
		Stage	Weight	fu	li	ci	cu	cl	ol	la
<i>anterior band of terga 1-8, pointed microsculpture:</i>										
present, at		2-3	1	at	AT	AT	at	at	at	at
absent, AT										
<i>anterior band of tergum 9, pointed microsculpture:</i>										
present, au		2-3	1	au	AU	AU	au	au	AU	AU
absent, AU										
<i>urogomphus, pointed microsculpture:</i>										
present, av		2-3	1	av,AV	av	AV	av	av	av	av
absent, AV										
<i>epipleura 2-7, no. acc. setae:</i>										
15-20,aw										
25-35,AW1			1							
40-60, AW2		3	1	AW1	AW2	AW2	aw	aw	aw	aw

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
<i>sternite 8, no. acc. setae:</i>									
15-20, ax									
30-40, AX	3	1	AX	AX	AX	ax	ax	ax	ax
<i>sternite 9, no. acc. setae:</i>									
5-7, ay									
1-2, AY	3	1	ay	ay	ay	ay	ay	AY	AY

Table 57. Distribution of selected characters of adults among species of subgenus *Elaphrus* and evolutionary classification of the character states and their weight (taxa abbreviated: 'ma' = *margenicollis*, 'lh' = *lheritieri*, 'mi' = *minus*, 'vi' = *viridis*, 'hy' = *hypocrita*, 'ru' = *ruscarius*, 'le' = *lecontei*, 'ca' = *californicus*, 'fi' = *finitimus*, 'am' = *americanus* 'tu' = *tuberculatus*, 'ri' = *riparius*, 'co' = *comatus*, 'pa' = *parviceps*, 'ti' = *tibetanus*).

CHARACTER AND CHARACTER STATES				TAXA AND DISTRIBUTION OF CHARACTER STATES												
CHARACTER STATES	Weight	ma	lh	mi	vi	hy	ru	le	ca	fi	am	tu	ri	co	pa	ti
<b>Pronotum, no. acc. setae:</b>																
absent, a																
on head and pronotum, A1	2															
on pronotum only, A2	2	a	A2	A1	A1	a	a	a	a	(A1-2)	(A1-2)	(A2)	(A2)	a	A2	A2
<b>lateral margin, situation:</b>																
beaded, b																
not beaded, B	1	b	B	B	B	B	B	B	B	B	B	B	B	B	B	B
<b>shape of margin:</b>																
narrow, c																
explanate, C	2	c	C	C	C	c	c	c	c	c	c	c	c	c	c	c
<b>punctures size:</b>																
20-30 microns, d																
40-50 microns, D	2	D	d	d	d	d	d	d	d	d	d	d	d	d	d	d

(continued on next page)



Table 57 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES														
CHARACTER STATES	Weight	lh	ma	mi	vi	hy	ru	le	ca	fi	am	tu	ri	co	pa	ti
<i>punctures, pattern:</i>																
sparcer laterally, e																
roughly																
equidistant, E	2	e	E	E	E	e	e	e	e	e	e	e	e	e	e	e
<b>Prosternum,</b>																
<i>puncture density:</i>																
20–40 microns apart, f																
10–25 microns apart, F	1	f	f	f	f	f	f	F	F	F	F	f	f	f	f	f
<b>Elytra, main mirror, shape:</b>																
rectangular, g																
ovoid, G	1	g	G	G	G	g	g	g	g	g	g	g	g	g	g	g
<i>pit size:</i>																
moderate, h																
very large, H1	2															
absent, H2	2	h	H1	h	H2	h	h	h	h	h	h	h	h	h	h	h

(continued on next page)



Table 58. Distribution of selected characters of adults among species of subgenus *Elaphroterus* and evolutionary classification of character states and their weight (taxa abbreviated:'pun' = *punctatus*, 'au' = *aureus*, 'pur' = *purpurans*, 'an' = *angusticollis*, 'ul' = *ulrichi*).

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Weight	pun	au	pur	an	ul
<b>Pronotum, lateral margin</b>						
well outlined medially, a						
suggested medially, A	1					
absent, A'	1	a	a	A'	A	A
<b>postero-lateral puncture:</b>						
present, b						
absent, B	1	b	b	b	b	B
<b>Prosternal process, acc. setae</b>						
4-6, c						
0-2, C	1					
0-, C'	1	c	C	C'	C'	C'
<b>Metasternum, posterior margin, acc. setae:</b>						
present, e						
absent, E	1	e	e	e	e	E
<b>Elytral subsutural mirrors:</b>						
similar width, f						
one or two narrower, F	3	f	F	F	F	F
<b>Secondary sexual characters, (on fore tarsi and mid-tibiae):</b>						
expressed normally, g						
absent, G1	3					
more characters expressed, G2	3	G1	g	G2	g	g
<b>Mid-trochanter, no. setae:</b>						
1, h						
2, H	2	H	h	h	h	h
<b>Paramerers, setae size:</b>						
long, i						
short I	1	i	i	I	I	I

Table 59. Distribution of selected characters of larvae among species of subgenus *Elaphroterus* and evolutionary classification of character states and their weight (taxa abbreviated: 'au' = *aureus*, 'pur' = *purpurans*, 'an' = *angusticollis*, 'ul' = *ulrichi*).

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Stage	Weight	au	pur	an	ul
<b>Parietale, color:</b>						
mostly dark, j						
mostly pale, J	1-3	2	j	j	J	j
<b>Nota and terga, color:</b>						
dark brown, k						
with dark and pale parts, K	2-3	3	k	k	k	K
<b>Mandible, inner edge:</b>						
serrated, l						
smooth, L	1	1	l	L	L	L
<b>Parietale, sculpture dist.:</b>						
absent or almost, m						
10-25% dorsally, M						
50-80% dorsally, M'	1-3	1	m	M	M'	M'
<b>epicranial suture:</b>						
normal, n						
very short, N	1-3	1	N	n	n	n
<b>Pronotum, no. acc. setae:</b>						
25-35, o						
40-50, O		1				
55-65, O'	3	1	o	O	O'	O'
<b>Mesonotum and metanotum,</b>						
<i>no. acc. setae:</i>						
25-35, p						
45-55, P	3	1	p	p	P	P
<b>Terga 1-8, no acc. setae:</b>						
35-45, q						
40-60, Q	3	1	q	q	Q	Q

(continued on next page)

Table 59 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Stage	Weight	au	pur	an	ul
<b>Epipleuron:</b>						
narrow, r						
wide, R	3	2	r	r	r	R
<b>Urogomphus, no. very</b>						
<i>small acc. setae:</i>						
rare or absent, s						
numerous, S	2-3	2	s	s	S	S
<i>knob development:</i>						
small, t						
absent, T	2-3	2	t	t	t	T
<b>Abdominal epipleura 2-7,</b>						
<i>no. acc. setae:</i>						
about 20, u		1				
about 30, U		1				
about 40, U'	3	1	u	U	U'	U'

Table 60. Summation of steps used in determining character state polarities. A) Types of out-group evidence in determining a derived character state. B) Taxonomic category considered in out-group comparisons and their code. C) Type of out-group evidence used in determining a character state as derived for each character of listed tables. “\*” denotes that a limited number of divergent taxa were examined.

A) TYPES OF OUT-GROUP EVIDENCE

Type	Definition
I	A Character state that is unique to a group within a considered category, assuming the character is not ancestral to that category – autapomorphy.
II	A unique character state appearing in considered taxa and its sister lineage – synapomorphy.
III	As I or II, but state exists in distantly related groups (on basis of other characters) within a considered category – autapomorphy or synapomorphy with evidence of convergent evolution.

B) CATEGORY CONSIDERED AND CODE

Tribe: (T); Genus: (G); Subgenus: (S); Species group: (E)

C) TYPE OF OUT-GROUP EVIDENCE FOR EACH CHARACTER IN EACH TABLE

(continued on next page)

Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
I (T)	C*, D, G, I, J, K, L, N, U, V, V', X, Y-, AA1*, AA2*, AF1*, AF2*, AG, AL, AM, AO''	B', C, I*, J1, L*, P2*, Q2*, R3*, S, U2*, Y	A*, G		G2, R
III (T)	A, B, E, G, H, S, T, U', W1, W2, X1, X2, Y, Z, Z', AE, AH, AH', AI, AK, AN, AO, AO'	G, H, N, O, P, P1, Q, Q1, R1, R2, U1, W, X	B2		
I (G)	F, M, O, P, AB, AC, AD	A, D, F, K, Z,	C, D, D', E, J2, W, AP, AR	B, C	B, G1, H, K, T
II (G)	Q, R, U	B, E2, J2, M			

(continued on next page)

Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
III (G)	AJ	J2, R4, V, X, Y'	B1, H, K, L, Q, AB, AH, AL2, AQ2, AQ3, AR'	D, E	I
I (S)		T	J1, K3, O, R6, AA, AG1, AG2, AK2, AL1, AM2, AO, AQ1, AW1, AW2, AX	G, H1, H2, I, J, K1	A, E, S
II (S)	U-, AG-, AI-				F
III (S)	O-, Q-, R-, T-	E1, E3,	F-, K1, N1, N2, R5, R7, AI, AK3, AM1, AN, AT, AV	F, K2	A', L, M', O, O', P, Q, U, U'

(continued on next page)



Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
I (E)			I, J3, K5, P, R3, R5, X, Y, Z, AC, AD, AE, AF, AJ, AS, AY		J, M
II (E)			M		C, C'
III (E)			K2, K4, R1, R2, S, T1, T2, AK1, AU	A1, A2	

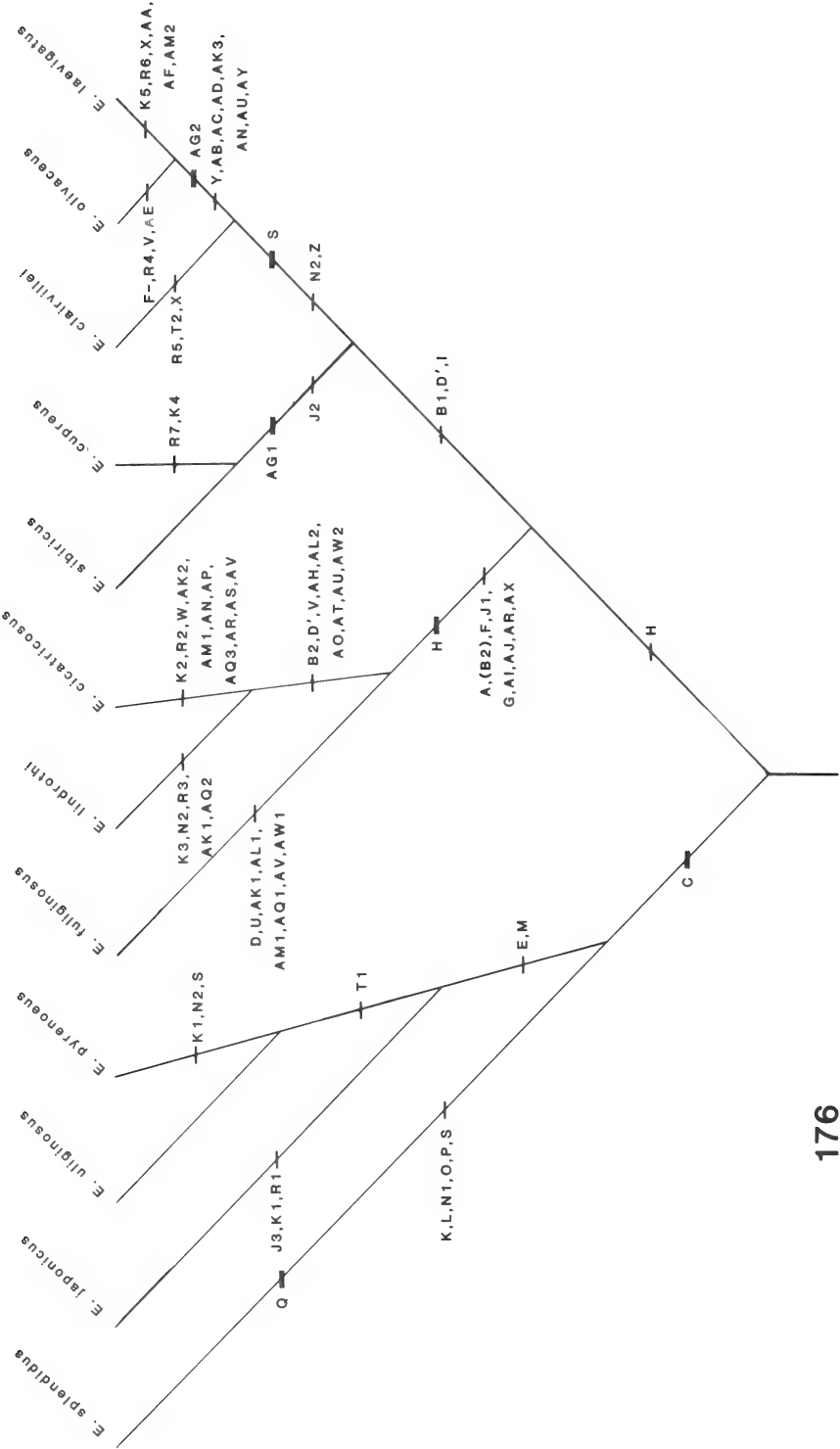


Fig. 176. Reconstructed phylogeny of species of subgenus *Neolaphrus* based on adults and larvae. Capital letters refer to derived states of coded characters (see Tables 52 to 56). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

## PHYLOGENY OF ELAPHRINI

**Monophyly of Elaphrini**

The tribe Elaphrini forms a monophyletic assemblage as shown by the following uniquely derived character states. Adults: presence of longitudinal keel-like microsculpture under the subapical portion of the elytron, and of lateral pairs of plates expanded apically into a curved row of points on abdominal tergum 7 (see figures 4 to 7 in Bauer, 1973). These two structures appear functionally related (Lindroth, 1954; Bauer, 1973, 1976), but are apparently not sound-producing organs (Forsythe, 1978). Larvae: the urogomphus of the second and third instar larvae, (except that of *E. ulrichi*) with unusual pattern of large and small projections (Figs. 93 to 103).

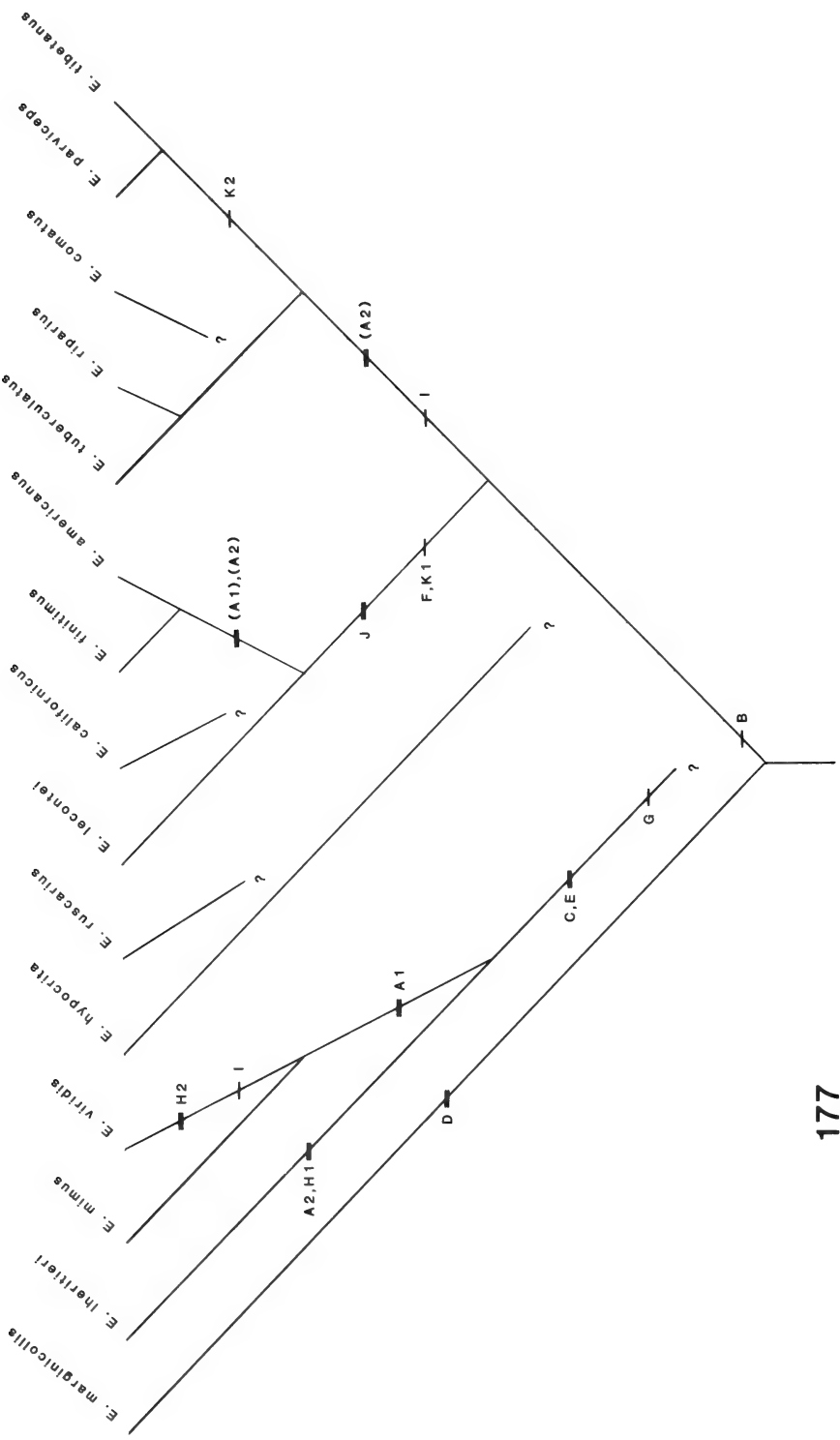
**The elaphrine sister group**

The Elaphrini are not clearly positioned in the general system of the Carabidae, as shown by the following points of view. Jeannel (1941, 1942) discussed relationships of the elaphrines to other carabid tribes. He put them near Migadopini, a tribe of the southern hemisphere. Among his "Caraboidea Simplicia", adults of Migadopini and of Elaphrini share similar setose parameres, probably an ancestral state shared with various older lineages of carabids and other adepagous beetles, and with lineages of similar age (Broscini, Patrobini, Nomiini, Melaenini and Scaritini). However, elaphrine adults have narrow metepimera, a feature which locates the tribe near Jeannel's "Caraboidea Limbata, Scrobifera or Stylifera". Therefore, Elaphrini are probably not related to Migadopini.

Bell (1967) put the Elaphrini in the Isopleuri with Loriccerini, Scaritini and Cicindelini. However, the Isopleuri are not defined by any shared derived character state. Ball's (1956) study of broscine male genitalia gave the best evidence about relationships of Elaphrini with Stylifera. The complex posterior sclerites x and y seen in Broscina (Figs. 36a, b) seem homologous with the elaphrine stylet and anterior cup-shaped sclerite. Sclerite x of the Broscina is made of two long dorsal adjacent sclerites and is membranous ventrally; the ejaculatory duct penetrates the posterior end. This stylet is also found in males of Melaenini, (Figs. 37a, b) a little known tribe. In Melaenini, the sclerite x is similar to that of *Diacheila*. Moreover, in adults of Melaenini, some Broscini and Elaphrini (except those of *Diacheila*), the antero-medial portion of setigerous punctures of elytron is elevated and cone-like. Adults of Melaenini and Elaphrini also have an oblique comb dorso-apically on the midtibia, but lack a dorsal brush on the midtibia (Erwin, 1978). However, adults of Elaphrini differ from those of the Broscina and Melaenini in having disjunct middle coxae and narrow metepimera.

Sclerites x and y are probably uniquely derived states. Thus, the Elaphrini, Melaenini and the Broscina should be considered related. Because I have only this evidence. I cannot say if this state was lost or did not evolve in the remaining Broscini and other tribes with setose parameres, and if a long stylet-like sclerite x is derived relative to the shorter sclerite in males of Broscina.

In the general frame of carabid classification, the Elaphrini and its related groups, the Melaenini and the Broscina, are related to the Nomiini, Patrobini and remaining subtribes of Broscini. They share with most members of these tribes a posterior transverse impression behind the eyes (probably a derived state). Elaphrini may be the earliest lineage among these tribes. In adults of these tribes, the middle coxae are conjunct (a derived state).



177

Fig. 177. Reconstructed phylogeny of species of subgenus *Elaphrus* based on adults. Capital letters refer to derived states of coded characters (see Table 57). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

### Relationships among genera and subgenera of Elaphrini

*Adults*.— The following derived character states show that species of *Blethisa* and *Elaphrus* have a common ancestor, exclusive of *Diacheila*: median lobe of males sharply divided into thickly (ventral and basal surface) and thinly (lateral and dorsal surfaces) sclerotized portions; stylet of internal sac extended anterad to base of ejaculatory duct for muscle attachment; setigerous punctures of interval 3, 5 and 9 cordiform, when completely outlined, and elevated in anterior portion of emargination. *Diacheila* is the sister group of the above genera.

Each genus is monophyletic as shown by uniquely evolved character states (see Fig. 175a for details). The ancestors of *Diacheila* evolved narrow and scimitar-shaped setae on the anterior margin of the prosternum; those of *Blethisa* evolved 8-shaped frontal grooves; and those of *Elaphrus* evolved elytral pits and mirrors, and ominent eyes.

The species of *Elaphrus* were grouped by Semenov (1926) into five subgenera of which four are retained here. The naturalness of each subgenus is clearly suggested by character states indicated in Fig. 175a. The main evidence for relationships between subgenera of *Elaphrus* is based on reduction of apical setae on apical sclerites of the stylus of the ovipositor. Females of *Arctelaphrus* have two very small setae, those of the ancestor of *Neoelaphrus* lost one, and those of *Elaphroterus* and *Elaphrus* lost both (for details see Fig. 175a).

*Larvae*.— Synapomorphies confirm most groups of adults, but they are few and of low weight (for details see Fig. 175b).

A close relationship of *Blethisa* and *Elaphrus* is suggested by the following shared derived states: increased number of accessory setae on all sclerites of the second and third instar larvae and larger seta on galeomere 1. In these two characters, larvae of *Diacheila* are more similar to members of other tribes. The naturalness of each genus was demonstrated by uniquely derived character states indicated in Fig. 175b.

The common ancestor of *Elaphrus* and *Elaphroterus* evolved a shorter head, shorter epicranial suture, and two or more rows of setae in the apical 0.3 of the inner dorsal surface of the stipes. However, I failed to show if *Neoelaphrus* is ancestral to all subgenera, shares a recent ancestor with *Arctelaphrus* or with the remaining subgenera.

### Relationships among species of subgenus *Neoelaphrus*

*Adults*.— The species of *Neoelaphrus* are arranged in three groups. The naturalness of each group is suggested by the following shared derived character states (see Fig. 176 for details). Adults of the ancestor of the *uliginosus* group gained four to six impressions on each side of the pronotal disc, and the pronotal lateral margin in lateral view became sinuate near the middle; those of the *fuliginosus* group gained a cuticular projection at the base of the anterior and posterior spurs of the male foretibia, and evolved a thick (100 microns) eye cornea; those of the *cupreus* group evolved a narrower (10 to 15 microns) bead on the lateral margin of the pronotum.

The main evidence for the relationships between these three groups is area of termination of the fringe of the pronotal posterior margin. In members of *Diacheila* and *Arctelaphrus* the fringe is terminated behind the postero-lateral impression (30 to 120 microns from hind angle). Thus, the *fuliginosus* and *cupreus* groups are sister groups since they share the following derived state: fringe of posterior margin of pronotum ended before postero-lateral impression (200 to 250 microns from hind angle).

The *uliginosus* group has four and probably five known species. *E. uliginosus* and *E. pyrenoeus* are sister species as suggested by the thick and twisted apex of the male median lobe in dorsal view. *E. japonicus* is closely related to the *E. uliginosus* - *E. pyrenoeus* lineage as shown by the major development of impressions on the pronotum.

The *fuliginosus* group has three extant species. Of these, *E. lindrothi* and *E. cicatricosus* share the following derived characters: loss of the bead on the lateral margin of pronotum, and of accessory setae on abdominal sterna 5, 6 and 7 of both sexes.

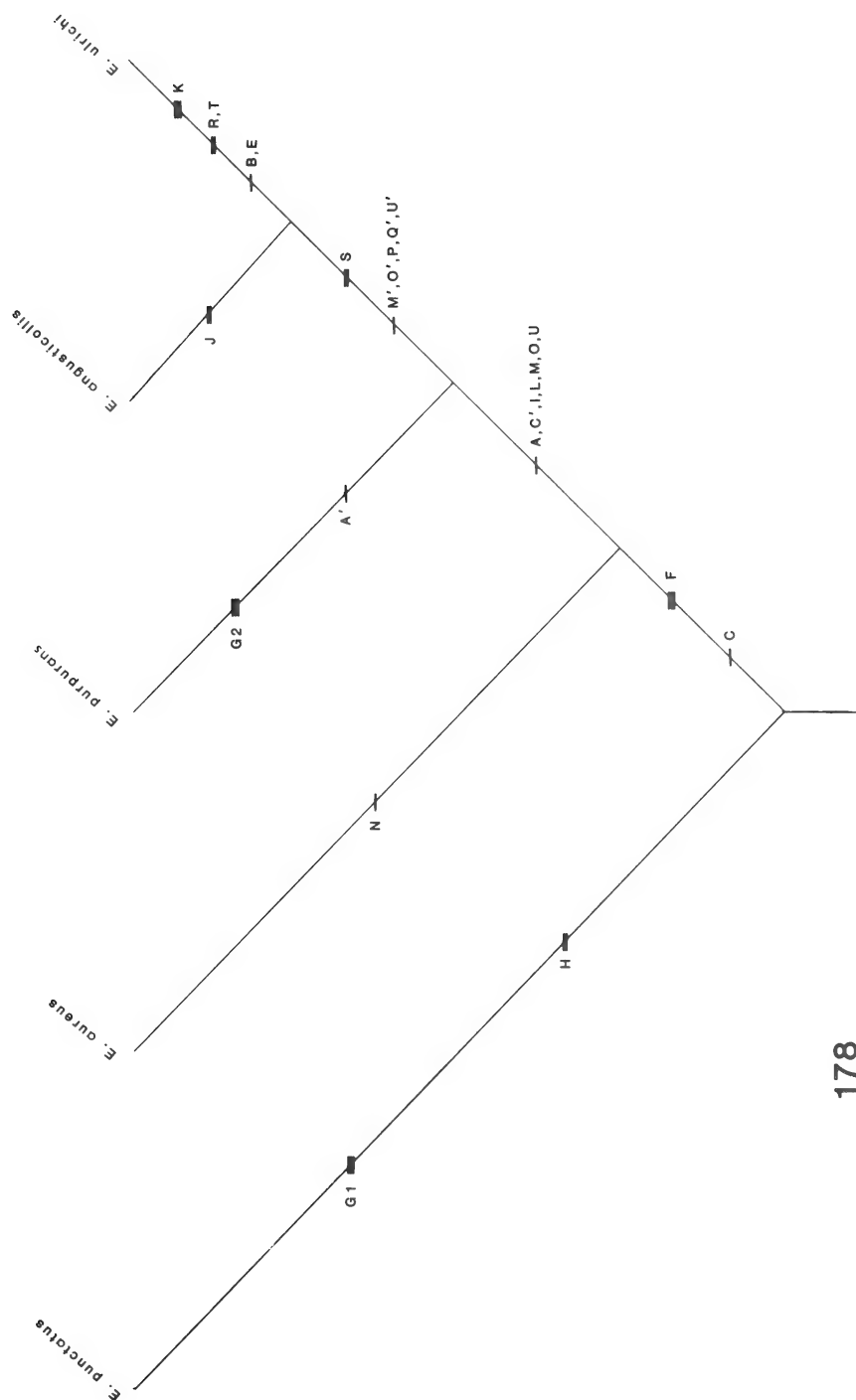
The *cupreus* group has five extant species, which are arranged in two subgroups. Adults of the ancestor of the *sibiricus* subgroup evolved a very elongate and wide (in lateral view) apex of the male median lobe. Those of the *clairvillei* subgroup gained a brilliant dorsal surface (lack of microsculpture, or presence of meshes under smooth transparent layer), and the lateral ridges of the elytral pits became fused. In the *sibiricus* subgroup, two species are known: *E. cupreus* and *E. sibiricus*. The *clairvillei* subgroup has three species. Of these, adults of *E. olivaceus* and *E. laevigatus* evolved dense pleural punctation, a short apex of the median lobe, and fine dorsal punctures, and lost the cuticular projection at the base of inner spur on male midtibia.

*Larvae*.— Two groups were studied: the *fuliginosus* and *cupreus* groups (Fig. 176). Naturalness of the *fuliginosus* group is shown by an unusual abundance of accessory setae on many sclerites, by reduction of sculpture on parietale, by a shorter epicranial suture, and by a much paler parietale. I failed to find shared derived character states between members of the *cupreus* group. Among the three species of the *fuliginosus* group, *E. lindrothi* and *E. cicatricosus* share the following derived character states: abundant accessory setae on many sclerites, reduced pointed microsculpture on anterior bands of terga, and loss of teeth on nasale. Less can be said about relationships between species of the *cupreus* group, except that adults of *E. olivaceus* and *E. laevigatus* share the following derived character states: marked development of microsculpture on the parietale of the first instar larvae, lack of microsculpture on the pronotum laterally and on the anterior band of tergum 9, and reduction of accessory setae on the sternite 8.

Reconstructed phylogeny based on adults and larvae, when shown, is fully congruent. The contribution of larval character states to the reconstruction was limited and less significant because of low weight of most character states.

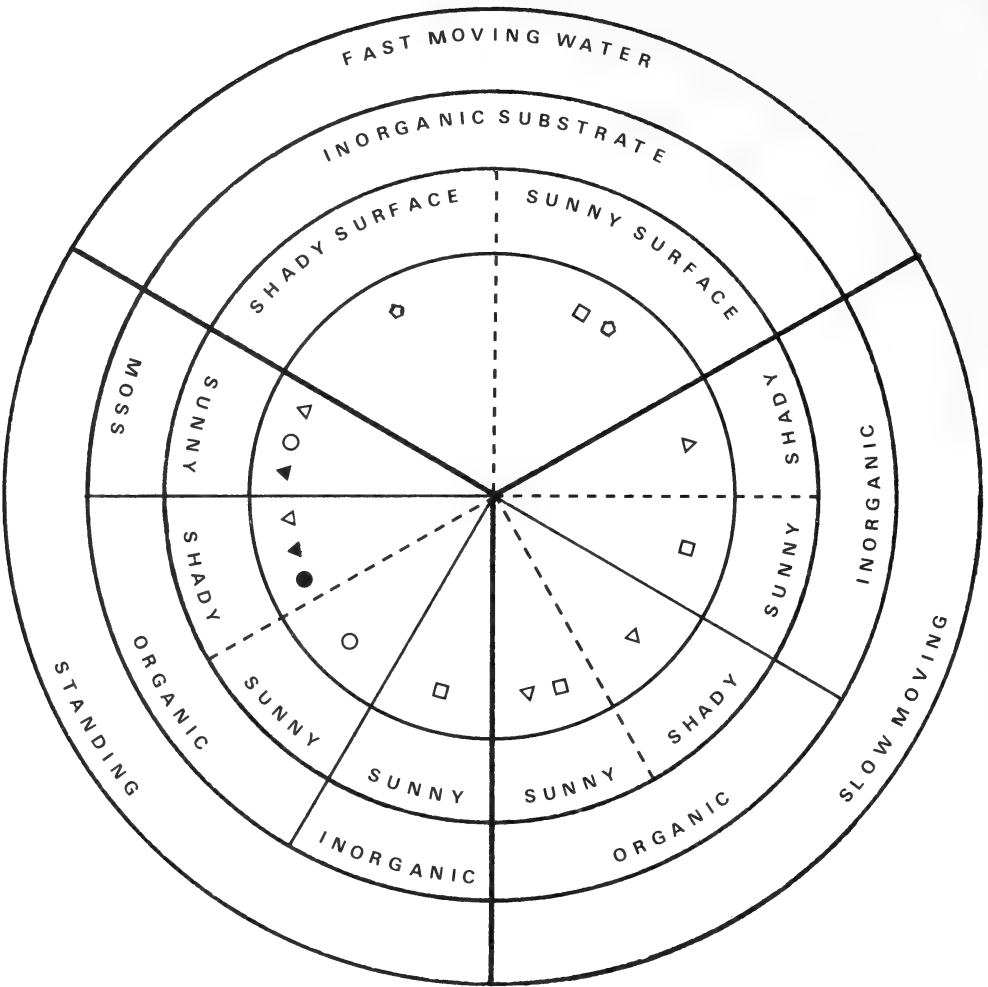
### Relationships among species of subgenus *Elaphrus*

*Adults*.— The 15 extant species are arranged in five groups. Except for the *marginicollis* group with one species, the remaining four groups are closely related as shown by the incompletely beaded lateral margin of the pronotum. The naturalness of each group, except for the *hypocrita* group, is shown, but relationships between these groups could not be demonstrated (for details see Fig. 177). Adults of the *lheritieri* group are highly differentiated. The three extant species share the following derived character states: explanate lateral margin of pronotum, uniformly dense punctures on pronotum, and oval-shaped main mirror of elytron. The naturalness of the *hypocrita* group could not be shown. However, its two species are similar to one another and may be closely related. The last two species groups are probably closely related, but I failed to find shared derived character states. The *lecontei* group comprises four species having the following derived character states: very dense punctures on proepisternum and on abdominal sterna; abdominal accessory setae less abundant in females. The *riparius* group comprises five closely related species sharing the following derived character state:



178

Fig. 178. Reconstructed phylogeny of species of subgenus *Elaphroterus* based on adults and larvae. Capital letters refer to derived states of coded characters (see Tables 58 and 59). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines high.



- Diacheila ●
- Blethisa ▲
- Arctelaphrus ○
- Neaelaphrus △
- Elaphrus □
- Elaphroterus ☆

Fig. 179. Correlation diagram for character states of habitat, and circadian activity (diurnal open figures, nocturnal black figures) among species of Elaphrini.



abdominal accessory setae extended to lateral edge of sterna 5 and 6 at least.

In the *lheritieri* group, *E. viridis* and *E. mimus* are sister species. They share a similar distribution of accessory setae on the dorsal surface, and both have lost pronotal impressions.

In the *lecontei* group, *E. finitimus* and *E. americanus* are almost indistinguishable. Therefore I assume they are sister species. I have no evidence for retracing relationships of *E. californicus* and *E. lecontei*.

In the *riparius* group, there are two pairs of closely related sister species. Firstly, *E. riparius* and *E. tuberculatus* are assumed to be related as they are almost indistinguishable (development of pointed sculpture on abdomen of some adults of *E. tuberculatus* suggest this close relationship). Secondly, *E. parviceps* and *E. tibetanus* are closely related as shown by the few punctures on the abdominal sterna. The position of *E. comatus* is not clear.

*Larvae*.— As characters were few, and their states of lowest weight, I did not attempt a phylogenetic reconstruction based on larvae.

### Relationships among species of subgenus *Elaphroterus*

*Adults*.— Members of this subgenus are arranged in three groups (Fig. 178). Of these, the *aureus* and *purpurans* groups share the following derived characters: unequal subsutural mirrors; reduced or obliterated lateral margins of pronotum. Relationships among the three species in the *purpurans* group are not clear.

*Larvae*.— Only larvae of the *aureus* and *purpurans* groups are known. Study of larval characters confirm both groups. Larvae of the single species of the *aureus* group have an unusually short epicranial suture, and those of the three species of the *purpurans* group share the following derived states: smooth inner edge of mandibles of first instars; numerous accessory setae on pronotum and tergal epipleuron of second and third instars. Among the three species of the *purpurans* groups, *E. angusticollis* and *E. ulrichi* are closely related as shown by many derived characters (Fig. 178), although their larvae appear quite dissimilar.

The phylogenies based independently on adults and larvae are congruent and complementary. Using data of both stages, phylogeny of the species of this subgenus was reconstructed (for details see Fig. 178).

## CLASSIFICATION OF ELAPHRINI

Classification involves establishment of formal ranks and location of taxa under study within a system of higher taxa. In the phylogenetic system of Hennig (1966), taxa are monophyletic and holophyletic (Ashlock, 1975) and are ranked according to relative age of origin, inferred from distribution of character states. In the so-called "evolutionary" system taxa are monophyletic (holophyletic) or paraphyletic and are ranked according to criteria of divergence, diversity and relative age (Simpson, 1961; Mayr, 1969).

Supra-specific ranks used in this study are four: tribe, genus, subgenus and species group. This number of ranks seems sufficient to encompass the limited diversity and to portray the major features of evolution of the species. The data presented establish that each higher taxon is clearly delimited by uniquely derived character states, and that each of the three groups, currently ranked as a genus, is clearly distinguished from all others. At a higher level this applies to the tribe Elaphrini as currently accepted, and at a lower level to the subgenera of *Elaphrus*. Thus, in recognizing taxa, I have adhered to the principle of monophyly and holophyly of the cladistic system.

I have not felt it necessary or desirable to recognize a formal taxon to include *Blethisa* and *Elaphrus* apart from *Diacheila*, nor to group the subgenera of *Elaphrus*, because of the limited diversity of the Elaphrini.

## ZOOGEOGRAPHY OF ELAPHRINI

### Introduction

Elaphrine beetles inhabit temperate and boreal zones of the northern hemisphere. To reconstruct the past geographical history of the group, I use working principles presented by Darlington (1957) as reviewed by Erwin (1970). Darlington (1957) presented a list of clues which may help in inferring the probable past history of a group. They are best used in combination, as extinction and recession affect the value of one or more clues.

1. The place of origin may be indicated by the area of greatest diversity. Highly diverse faunas in a given area are probably the result of longer evolutionary history in that area than in other areas where the faunas are little diverse.
2. The place of origin may be indicated by the area of greatest differentiation. Highly differentiated faunas are probably the result of longer evolutionary history in that area than in other areas where the faunas are little divergent.
3. The extent of area probably increases with age of the taxon. The older the taxon, the more geological and paleoenvironmental events would allow it to invade previously inaccessible areas.
4. Present geographic and/or climatic distribution of taxa of older lineages probably indicate the area of origin and/or the probable climatic zone of the common ancestor.
5. The present distribution of vicariant taxa may indicate area of origin and/or the paleoenvironmental events that brought about these vicariant taxa.
6. Fossils may indicate the area of origin and/or the time scale for the reconstruction of past history or the taxa.

I first present evidence gathered from extant and fossil specimens. I then postulate the probable place of origin of elaphrine beetles and retrace the histories of elaphrine genera and sub-genera.

### The Evidence

*Distribution patterns.*— The number of species is nearly equal between the Palaearctic and Nearctic Region for elaphrine genera and *Elaphrus* subgenera *Arctelaphrus* and *Neoelaphrus* (Table 61). However, the subgenus *Elaphrus* is more diverse in the Nearctic Region while *Elaphroterus* is more diverse in the Palaearctic Region. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group is in the Palaearctic, the *fuliginosus* group is in the Nearctic, and the *cupreus* group is about equally represented in Palaearctic and Nearctic Regions.

Within continents, the genera and subgenus *Elaphrus* are most diverse on the Pacific side of both land masses (Table 62). However, the only member of *Arctelaphrus* is Holarctic, the subgenus *Neoelaphrus* is more diverse in Asia and eastern North America, and *Elaphroterus* is more diverse in Europe and western North America.

The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group is more diverse in Asia, the *fuliginosus* group is restricted eastern North America, and the *cupreus* group is more diverse in Asia and western North America.

Table 61. Number of extant species of genus-group taxa of Elaphrini confined to or shared between the Palaearctic and Nearctic Regions.

Taxa	Palaearctic	shared	Nearctic	Total
<b>A. Genera</b>				
<i>Diacheila</i>	3	2	2	3
<i>Blethisa</i>	4	2	6	8
<i>Elaphrus</i>	19	4	19	34
Total	26	8	27	45
<b>B. Subgenera of <i>Elaphrus</i></b>				
<i>Arctelaphrus</i>	1	1	1	1
<i>Neoelaphrus</i>	7	0	6	13
<i>Elaphrus</i>	7	2	10	15
<i>Elaphroterus</i>	4	1	2	5
Total	19	4	19	34
<b>C. Groups of <i>Neoelaphrus</i></b>				
<i>uliginosus</i>	5	0	0	5
<i>fuliginosus</i>	0	0	3	3
<i>cupreus</i>	2	0	3	5
Total	7	0	6	13

*Climatic patterns.*— In the following discussion, I use broad climatic zones. These zones are briefly defined as follows. The warm temperate zone is characterized by mild winters and long hot summers (in eastern North America this zone extends from southern Pennsylvania to the Gulf of Mexico). The cold temperate zone is characterized by cold winters and hot summers (in eastern North America this zone extends from northern New England to Québec City). The boreal zone is characterized by long cold winters and short cool summers (in eastern North America this zone extends from the Gulf of St. Lawrence to the northern treeline). The northern half of the boreal zone is termed the subarctic zone. The arctic zone is characterized by short cool summers and long, very cold winters.

Species of elaphrines are generally widespread in one or more climatic zones. Elaphrines are found from the southern edge of the tundra to the southern half of the warm temperate zone (Table 63). None is known from subtropical or tropical zones. Adults of most species live at low elevations, but those of a few species are in the subalpine zone. Adults of *Elaphrus* and *Blethisa* are known from the above climatic zones, but those of *Diacheila* are found in the arctic, subarctic or the subalpine zone. Subgenera of *Elaphrus* range in the above climatic zones except for the sole species of *Arctelaphrus*, which is restricted to subarctic and subalpine zones. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group has northern warm temperate, cold temperate and boreal species; the *fuliginosus* group has northern warm temperate and cold temperate species; the *cupreus* group has warm temperate, cold temperate and boreal species.

*Diversity in North America.*— I present a synopsis for only this continent because it has a varied elaphrine fauna and the distribution patterns are better known to me. However, the general observations presented below are similar for the well collected western Palaearctic





Fig. 180. Summary of probable zoogeographical events during the evolution of subgenus *Neoelaphrus* in Eurasia and North America. Their phyletic position is shown in Fig. 176. Climatic conditions are for Alaska for each period. The North American and Eurasian epicontinental seas are expressed as thick lines and the presence of land bridges as dotted lines in function of time.

Table 62. Number and distribution of extant species of genus-group taxa of Elaphrini within the Palearctic and nearctic Regions.

Taxa	Palearctic			Nearctic		
	Europe	shared	Asia	West	shared	East
<b>A. Genera</b>						
<i>Diacheila</i>	2	2	3	2	1	1
<i>Blethisa</i>	1	1	4	6	3	3
<i>Elaphrus</i>	10	6	16	15	7	11
Total	13	9	23	23	11	15
<b>B. Subgenera of <i>Elaphrus</i></b>						
<i>Arctelaphrus</i>	1	1	1	1	1	1
<i>Neoelaphrus</i>	3	2	7	3	2	5
<i>Elaphrus</i>	3	2	6	9	4	5
<i>Elaphroterus</i>	3	1	2	2	0	0
Total	10	6	16	15	7	11
<b>C. Groups of <i>Neoelaphrus</i></b>						
<i>uliginosus</i>	2	1	5	0	0	0
<i>fuliginosus</i>	0	0	0	0	0	3
<i>cupreus</i>	1	1	2	3	2	2
Total	3	2	7	3	2	5

Region. The most notable fact is that diversity is high in all regions between the subarctic and the northern half of the warm temperate zone (excluding the foggy, cool, maritime zones of the Pacific coast and Newfoundland, the subdesert regions, and most of the Canadian Shield) and is followed by an abrupt decrease beyond these climatic zones. In the north around the Mackenzie Delta, adults of seven species are known, but north of the tree line, 70 kilometres away, only two species are known. In Maryland, five species are known, but in Virginia southward, only two are recorded. North of the Mogollon rim in the southwest United States, three species are known, but south of it in the desert area, only one specimen of one species has been collected. In California in the San Francisco vicinity, six species are known, but near Los Angeles, only two are known. Within the area of high diversity, over a surface of about 500 square kilometres, one can expect between five and nine species. Diversity is slightly higher in western North America. The main centres of diversity are: northern California, Yukon, western Northwest Territories, Colorado, and southern Québec.

*Dispersal potential.*— During their active season on sunny days, adults of *Elaphrus* often fly. Power and frequency of flight is clearly suggested by the abundance of captures of adults of all known New England species near subalpine and alpine bodies of water on Mount Washington, N.H., Mount Mansfield, Vt., and White Face Mountain, N.Y. Although these areas are not normally occupied (*i.e.*, no immatures were found), locality labels, Darlington's observations (pers. comm.) and my own, clearly suggest that such individuals (stragglers) have enough control of their flight to land near suitable habitats.

*Habitat diversity.*— Data presented here are summarized in Fig. 179. Elaphrine beetles are closely associated with water, except for those of *D. polita*. Adults of *D. arctica* live near

Table 63. Number and distribution of extant species of genus-group taxa of Elaphrini in climatic/geographic zones.

Taxa	Arctic	Boreal	Temperate cold	Montane warm	
<b>A. Genera</b>					
<i>Diacheila</i>	2	1	0	0	0
<i>Blethisa</i>	1	5	2	2	2
<i>Elaphrus</i>	3	14	19	16	12
Total	6	20	21	18	14
<b>B. Subgenera of <i>Elaphrus</i></b>					
<i>Arctelaphrus</i>	1	1	0	0	0
<i>Neoelaphrus</i>	1	5	8	6	4
<i>Elaphrus</i>	1	5	7	7	5
<i>Elaphroterus</i>	0	3	4	3	3
Total	3	14	19	16	12
<b>C. Groups of <i>Neoelaphrus</i></b>					
<i>uliginosus</i>	0	1	2	1	3
<i>fuliginosus</i>	0	0	2	3	0
<i>cupreus</i>	1	4	4	2	1
Total	1	5	8	6	4

marshes of icy standing water on abundant mosses. Adults of *D. polita* occur under leaf litter, and show many adaptations for digging – probably an early step toward inhabiting subterranean habitats. Specimens of all species of *Blethisa*, except perhaps of *B. eschscholtzi*, are associated with cold standing water. Adults of one species live on thick *Sphagnum* moss carpets, whereas those of other species occur in the shade of dense *Carex* vegetation or on sun-exposed places with open mud and low moss carpets. Adults of *Blethisa* and *Diacheila* are nocturnal, but those of *Elaphrus* are diurnal. Specimens of the sole known species of *Arctelaphrus* live on thick moss carpets. As far as is known, specimens of *Neoelaphrus* occur near rivers or standing water. Individuals of most species live on organic soil, those of *E. lindrothi* are on wet clay flats. The habitat of most species has little or no vegetation, except that of *E. laevigatus* and *E. clairvillei*. Adults of about half of the species are found in sun-exposed areas, but those of others are in deep shade. Specimens of the subgenus *Elaphrus* occur on sun-exposed surfaces. Adults of most species are riparian, but those of a few live near standing water which may be cool or warm. Adults of a few species are restricted to beaches with high organic content, but those of most live on sand silt, clay, or a mixture of these soils. Adults of two species are found near alkaline waters. As far as is known, adults of all species of this subgenus are active on low beaches. Adults of *Elaphroterus* are riparian (the habitat of *E. punctatus* is not known). Their preferred habitat may be either sun-exposed or shaded. Specimens of these species, as far as known, live on middle and upper beaches of river banks.

*Fossil evidence.*— I studied numerous fragments of *Elaphrus* adults of the following species dating from the last glaciation: *E. lapponicus*, *E. clairvillei*, *E. olivaceus*, *E. parviceps*, *E. americanus* and *E. californicus*. Specimens of these taxa match extant specimens, and those of

*E. parviceps* and *E. clairvillei* are assigned to extant geographical races. Therefore, there is no evidence of structural changes since the last glacial retreat. These conclusions are backed by Matthews (1974b), Coope (1970) and Lindroth (1969). I also examined excellent fragments of adults of Late Miocene age (between six to ten million years before present—mybp). Some fragments match extant species (*E. lapponicus*, *E. angusticollis angusticollis*), most extant specimens of *E. riparius* complex (mostly *E. tuberculatus*), one partially present-day adults of *E. sibiricus*, and some extinct species. Matthews (1970, 1974a, 1974b and 1976) observed little or no differentiation among other lowland carabids of the same age and locality.

*Synopsis of past geological and climatic events.*— North America and Europe were in contact until the end of the Cretaceous (Dietz and Holden, 1970). Early in the Tertiary, Eurasia was linked with North America by Alaska (Hopkins, 1967). The area between eastern Siberia and Alaska is called Beringia.

Epicontinental seas bisected Eurasia and North America in the Late Cretaceous. In North America, a sea extended along a north-south axis east of the Rockies until the end of the Cretaceous (Williams and Stelck, 1975). In Eurasia, a sea extended along a north-south axis east of the Urals until the Early Eocene (Hopkins, 1967). Beringia was probably an exposed land bridge from the Paleocene (63 mybp) until the late Pliocene (3.0 mybp) when a sea transgressed the bridge (Hopkins, 1967; Matthews, 1979). The bridge was reopened only during some of the glacial periods.

The climatic reconstruction is taken mainly from Wolfe (1972) whose study deals with Alaska, a most crucial area. I also have more confidence in his conclusions about past climate, based on his analysis of taxa and leaf physiognomy, than I have in the work of other authors. Climate in the Late Cretaceous and Paleocene was equitable, with subtropical conditions extending into Alaska. Beringia was then as far north as it is today. The temperate zone was probably restricted to northernmost portions of Canada and central Siberia. During the Middle Eocene, Alaska became paratropical. The temperate zone became very restricted or disappeared (Matthews, 1979). From then on, the climate deteriorated until the Pleistocene. During the Late Eocene, the climate of Alaska was equivalent to that of the southern half of the warm temperate zone. During the Early Oligocene, Alaska was subtropical; by Middle Oligocene, it was cold temperate; but in the Late Oligocene, it was equivalent to that of the northern half of the warm temperate zone. During the Early Miocene, the climate of Alaska was cold temperate; by the Middle and Late Miocene, boreal conditions developed in northern Alaska, while southern Alaska remained cold temperate. During the Pliocene, boreal and subarctic conditions extended over Alaska, and by the Late Pliocene, arctic conditions developed, and along the Bering coast grassland appeared. During the Pleistocene, Alaska alternated between arctic and subarctic conditions.

### **Climatic Requirements of Ancestors of Major Lineages of Elaphrini**

By comparing climatic zones of earlier lineages of species of each higher taxon, one can suggest an hypothesis about the probable climatic tolerance of various ancestors (clue 4). Climatic adaptations of extant species of *Diacheila* suggest a relatively recent subarctic adapted ancestor, those of *Blethisa* a cold temperate or boreal adapted ancestor, the one of *Arctelaphrus* a recent subarctic-adapted ancestor, those of *Neoelaphrus* a warm temperate adapted ancestor, and those of subgenus *Elaphrus* and *Elaphroterus* a cold temperate adapted ancestor.



### Center of Origin

I believe that the center of origin of extant genera and subgenera of elaphrines was in the northern Pacific landmass. Evidence is derived from many of the clues presented above. To justify this statement, I first discuss Beringia as a secondary center of radiation in order to establish when elaphrines were there and at what state in their evolution. Then I discuss my reasons for choosing this region as the primary center of radiation.

*Beringian Center.*— Present diversity of genera and subgenera of elaphrines between North America and Eurasia is the same. Therefore, an earlier corridor-like (Simpson, 1953) bridge must have existed. Diversity and degree of differentiation of genera and subgenera are highest on the Pacific side of the continents. Therefore, it is probable that exchange occurred in that area (clues 1 and 2). Earlier lineages of subgenera suggest that ancestors of *Blethisa* and *Elaphrus* were adapted to the warm or cold temperate zone. Therefore, exchange probably occurred on a bridge with a similar climate (clue 4). The distribution of sister groups among warm temperate *Neoelaphrus* suggests a close association with the mixed mesophytic forest which evolved in northern Asia (clue 5). Finally, Pleistocene and Late Miocene fossils of *Elaphrus* suggest a slow evolutionary rate (clue 6). Therefore, the most probable center of recent infra subgeneric taxa is in northern Asia and/or northwestern North America. Beringia was warm temperate as early as the Middle Oligocene (30 Mybp), and because it was a wide land bridge then, it could have served as a corridor for dispersal of ancestors of *Blethisa* and of *Elaphrus* subgenera *Neoelaphrus*, *Elaphrus* and *Elaphroterus*. Presence on Beringia of ancestors of extant species of genus *Diacheila* and of *Elaphrus* subgenus *Arctelaphrus*, based on present evidence cannot be confirmed.

*Pacific Center.*— Since no extant species are adapted to the subtropical zone, the common ancestor of Elaphrini was probably adapted to temperate or colder climates (clue 4). Since genera and subgenera were probably evolved by Oligocene times, the origin of extant elaphrine genera probably goes back to the Late Cretaceous (clues 3 and 6). During the Late Cretaceous cool temperate conditions existed in Alaska (Matthews, 1979), and North America and Eurasia were dissected by north-south epicontinental seas. Therefore, exchange between Asia and Europe, or between western North America and eastern North America was minimal. If the center of origin was on the Atlantic side of both continents, much exchange would have occurred between Europe and eastern North America as both continents were still broadly connected. Moreover, elaphrines would show a similar distribution and differentiation pattern to that of the Anisodactylina (Noonan, 1973) which are most diverse on the Atlantic side of the continents. Therefore, a northern Pacific center is more compatible with the evidence. This distribution is also more compatible with the probable center of evolution of its Asiatic sister groups, the tropically-adapted Melaenini and mountain-adapted Broscina. By Eocene times, ancestors of many elaphrine lineages may have been segregated in restricted and isolated temperate enclaves in Siberia and Beringia along the Arctic coast.

### Evolution of Habitat Preferences among Elaphrine Genera and Subgenera

As all elaphrines, except adults of *D. polita*, are associated with wet environments, the immediate ancestor of elaphrines most probably was associated with wet soils. I postulate that this ancestor was nocturnal (as adults of less derived *Blethisa* and *Diacheila* are nocturnal or crepuscular) and lived near standing water among moderately short vegetation. This habitat matches quite closely that of *D. arctica* and most extant species of *Blethisa* (clue 4). The main evolutionary step was taken by the immediate ancestor of *Elaphrus* as it became a diurnal

predator on open surfaces with little vegetation to obscure vision. Eyes of adults of *Elaphrus* are indeed large with wider angle of vision and more numerous ommatidia and those of *Diacheila* and *Blethisa*. The cellular arrangement is of photopic type (Kuster, 1979). Since adults of many species belonging to older lineages of *Elaphrus* are associated with moss carpets, the ancestor may have been adapted to such habitats. The single species of *Arctelaphrus* is found in a habitat similar to that postulated for the ancestor.

The habitat of species of earlier lineages of *Neoelaphrus* fits the above description (*E. uliginosus*, and *E. pyrenaicus*). However, younger lineages of *Neoelaphrus* invaded shaded habitats (*E. cupreus*, *E. lindrothi*, *E. clairvillei*, and *E. laevigatus*). Species of the *fuliginosus* group are partly riparian, and those of the *cupreus* group have riparian species (the *cupreus* subgroup) and standing water species (the *clairvillei* subgroup). Adaptation to standing water habitats is considered secondary as these became available again after evolution of the more cold hardy elements of the *cupreus* group.

The common ancestor or species of subgenera *Elaphrus* and *Elaphroterus* became adapted to substrates low in organic matter. The ancestor of species of subgenus *Elaphrus* remained adapted to the wet habitats, and invaded different and finer substrates. The ancestors of species of *Elaphroterus* became adapted to habitats near moving waters and to the moist section of beaches.

### Past History of Elaphrini

Based on the median lobe of males, Elaphrini are probably related to Broscina and Melaenini. The relationships of elaphrines with each of above groups is not clear. The Broscina are diverse in mountains of warm temperate and subtropical Asia, and the extant Melaenini in African and Asian tropics. Thus, the elaphrine ancestor might have been subtropical. Since elaphrines are not found near subtropical regions, the immediate elaphrine ancestor probably evolved in Late Cretaceous and survived in warm-temperate areas where it became diverse and gave rise to ancestors of extant genera and subgenera. The temperate adaptation of elaphrines and their absence from the subtropical areas where the common ancestor probably evolved might best be explained by the taxon cycle theory (Wilson, 1961).

Wilson's taxon cycle can be briefly summarized as follows. Invaders from zones of high diversity (larger land masses in Wilson) establish themselves in a zone of lower diversity (smaller and younger islands in Wilson) and become ecologically released (islands, in Wilson, are younger and support unbalanced faunas, and as a consequence, new comers are likely to increase ecological amplitude). These invaders evolve and, in turn, may be displaced by more recent invaders from regions of high diversity (new invasion from larger and older land masses in Wilson) and adapt to new niches with lower diversity (mountain forests in Wilson) or, they may become extinct, or they may colonize and survive in a new zone (another island of similar or smaller size in Wilson) with similar or lower diversity. However, the descendants of the first invader are unlikely to invade an area of intensive competition pressures successfully (larger and older land masses in Wilson). Darlington (1943) alluded to this cycle (origin of shortwing species of mountain carabids), clearly referred to it later on (1957), and presented evidence based on phylogenetic data (1971). Erwin (1979) referred to this cycle and suggested a new name "Taxon Pulse", and stressed that evolutionary changes were generally in one direction (*i.e.*, toward extinction), and that speciation events are likely to be triggered by succeeding waves of invaders. Islands are not only geographical but ecological entities. They are generally areas with lower diversity and consequently of less intensive competition pressures (*i.e.*, an

island with unbalanced fauna, a recently formed life zone like the arctic region, a habitat with many open niches like a peat bog). Therefore, the important factor in orienting this cycle is the difference in diversity between climatic zones (altitudinal or latitudinal), land masses, or habitats. An interesting characteristic of areas with lower diversity is the unexpectedly high proportion of eurytopic species. Moreover, I do not feel that invaders should be generalists (Wilson, 1961; Darlington, 1971; Erwin, 1979), or land size important in giving rise to these cycles. Invaders in proximity of zones to invade may be specialized, but at least they are pre-adapted to cross a special barrier (water or mountain gaps, cold winters, different climatic regimes, special habitats). Land size ultimately affects diversity (Darlington, 1943), but is not always related to it (arctic regions are immense and yet very low in diversity).

I feel this theory can account for extinction of groups in regions or life zones of origin, and for their presence in younger regions or life zones than that of the lineage studied. Thus, the restricted and young temperate zone in Late Cretaceous may have been a zone of low diversity in which elaphrine radiation started. This theory has been used in studies of historical reconstruction of some groups of ground beetles (Allen and Ball, 1979; Erwin, 1979).

Present ranges of *Diacheila* species are along the tundra-treeline boundary. Degree of divergence and fossils studied (Pleistocene and Miocene samples) clearly suggest an origin older than the present arctic regions (estimated to be about 6 million years old). Marsh adaptations are not evolved in mountain regions (personal observations based on North American carabid fauna) but rather in lowlands. Their evolutionary history probably started in lowland marshy regions under milder climatic conditions. Extant species, as far as studied, are associated with habitats of low insect diversity, especially ground beetles. These habitats are probably places of low competition pressures for these beetles.

The history of species of *Diacheila* might be presented as follows. Early in the history of this genus, there might have been a radiation, as suggested by marked divergence between extant species. Perhaps many species became extinct following radiation of more successful competitors. A few descendant species survived, probably in a more recently evolved life zone (further north) either in marshy environments or more specialized niches. This cycle of extinction and/or displacement continued until tundra-adapted species evolved. The range of species of *Diacheila* may have extended in Pliocene time across Beringia, but I suspect Holarctic ranges were achieved in the Pleistocene during glacial periods after the ancestors of two extant species became adapted to tundra.

Present species of *Blethisa* are structurally divergent. Evolutionary rates, indicated by fossils of Late Miocene times, are slow. Therefore, the age of the immediate ancestor may be older than the boreal zone where most species are found today. The common ancestor may have originated during the late Cretaceous. Their infrequent presence in cold temperate regions suggests that extinction of ancestral descendants occurred in the temperate zone. However, in the boreal zone, a younger region with lower competition pressures, a few descendant lineages survived and even radiated. In time, new invaders established themselves in boreal regions and probably brought to extinction many species except for a few adapted to marshy environments of tundra-treeline boundary regions or marshes with low diversity (short *Carex* and *Sphagnum* bogs). Two extant species are Holarctic, one, a boreal species, probably invaded the Nearctic during the Pliocene, and another, an arctic species, spread across Beringia during the Pleistocene.

Miocene fossils of *Elaphrus* studied (at least adults of five species representing all subgenera) clearly suggest slow evolutionary rates. The structural divergence between most

species is marked. The past history of some species in some subgenera is more complex than suggested in present distribution patterns.

The oldest lineage is represented by one surviving species in the subgenus *Arctelaphrus*. This is a subarctic species. Since Pleistocene and Miocene fossils of this species show no sign of structural changes, I feel the history of species of this subgenus is much older than the subarctic zone. Thus, its ancestor probably evolved under milder climates. Today the absence of any species further south may suggest extinction of most descendants of the *Arctelaphrus* ancestor, possibly due to higher competition pressures in older and warmer regions or habitats. Present-day populations of *E. lapponicus* are found in a habitat of low diversity, especially of carabid beetles. During the Pleistocene, *E. lapponicus* became Holarctic and probably invaded Kodiak Island in the Late Pleistocene giving rise under repeated harsh glacial conditions of the refugium to *E. lapponicus obliteratus*.

The complex past history of the species of *Neolaphrus* presented below is summarized in Fig. 180. From the Late Eocene on, the temperate zone enlarged as the climate cooled. Therefore, in early Tertiary the ancestor of *Neolaphrus* probably spread over wider areas in an evolving warm temperate forest. By the Late Oligocene (25 mybp), the range of this ancestor extended over Beringia. Climatic conditions continued to deteriorate, and by the Middle Miocene (17 mybp) as Beringia was becoming boreal, the ancestral population previously adapted to warmer conditions became divided. The Siberian stock gave rise to the ancestor of the *uliginosus* group while the North American stock gave rise to the common ancestor of the *fuliginosus* and *cupreus* groups.

Since no extant species of the *uliginosus* group are known in North America, it is probable that the boreal adaptations shown by *E. splendidus* are recent and not earlier than Late Pliocene. Events conducive to evolution of the extant species of this group cannot be interpreted in terms of the known distributions of extant species and past geological events. The *E. uliginosus* ancestor evolved in Europe, and, during glacial phases of the Pleistocene, extended toward southern France, leaving a subalpine stock that gave rise to *E. pyraoneus*. *E. uliginosus* seems to have been preadapted for invading mountains as suggested by the Apennine, Balkan and Tien-shan mountain populations. Of extant species, *E. splendidus* and *E. japonicus* belong to the oldest lineage. *E. japonicus* is closely associated with the mixed mesophytic forest (perhaps the ancestral habitat), and *E. splendidus* with cold temperate and boreal forests (perhaps a recent adaptation).

The North American stock of *Neolaphrus* gave rise to the extant species of the *fuliginosus* group that is closely associated with the mixed mesophytic forest (perhaps the ancestral habitat). Distribution of present species, and geological or climatic events cannot account for their speciation. The amount of divergence achieved suggests that the *fuliginosus* group evolved quite early in Late Miocene or Early Pliocene and that speciation probably occurred somewhere in Canada where the mixed mesophytic forest was widespread.

The North American stock of *Neolaphrus* also gave rise to the ancestor of the *cupreus* group. In time, a successful stock, adapted to cold temperate and boreal regions, evolved. This adaptation allowed the common ancestor to spread northward and across Beringia as early as the Middle Miocene (13 mybp). Thereafter, cooler conditions over Beringia effectively isolated the ancestor of the *cupreus* group into two stocks. The Asiatic stock became the ancestor of the *sibiricus* subgroup that gave rise to *E. cupreus* and *E. sibiricus*. The event conducive to this speciation process is unknown, since the extant ranges overlap extensively in Asia. The North American stock gave rise to the *clairvillei* subgroup adapted to standing water. This stock gave

rise to the boreal-adapted ancestor of *E. clairvillei* and to the common ancestor of *E. olivaceus* and *E. laevigatus*. Events leading to formation of these two ancestors are unknown. The common ancestor of *E. olivaceus* and *E. laevigatus* was probably widespread across the continent. However, following development in Pliocene time of colder conditions, the ancestral population could have become divided by cold temperate grassland and drier zones in the region of the Great Basin. The stock west of the Cascades gave rise to *E. laevigatus* and the eastern stock gave rise to *E. olivaceus*.

A phylogenetic reconstruction of extant members of the subgenus *Elaphrus* could only be attempted partially. However, enough information is available to suggest a taxon cycle in action north and south as well as a reversal of the cycle. The habitat and structural differentiation is great in this subgenus. Some species are widespread and in process of radiation (*E. californicus*, *E. finitimus*, *E. americanus*, *E. tuberculatus* and *E. riparius*). These species are successful in a wide range of latitudinal and altitudinal zones and belong to the two most highly evolved species groups. Some species show what is probably a taxon cycle in reverse (*E. finitimus* and *E. lecontei*) as some of their populations are successfully invading zones of high diversity farther south. The groups which evolved earlier (*marginicollis*, *lheritieri* and *hypocrita* groups) have species with restricted distributions. Despite the extreme southerly range of members of the *lheritieri* group, these species survive in habitats of low diversity. Their pattern does not represent a reversal of the taxon cycle, but rather the contrary. Both species of the *hypocrita* group are found in the warm temperate zone and their success seems moderate judging by their narrow latitudinal range. The ancestors of the *marginicollis*, *lheritieri* and *hypocrita* groups were probably widespread in warm temperate regions of the Palaearctic and the Nearctic region. The present disjunct distribution is probably relictual. On the other hand ancestors of the *lecontei* and *riparius* groups may have been separated into Palaearctic and Nearctic stock populations during the Early Miocene. The Nearctic stock evolved and gave rise to extant members of the *lecontei* group. The speciation events cannot be traced. Meanwhile those of the Palaearctic stock gave rise to present species of the *riparius* group whose speciation events cannot be traced also. However, during the Pleistocene, the most cold-adapted species (*E. tuberculatus* and *E. parviceps*) extended their ranges across Beringia into the Nearctic region during glacial events.

The ancestor of *Elaphroterus* was probably associated with fast moving waters of mountain origin. It probably invaded this unusual habitat from the Asiatic center of origin when much of the Asiatic mountain ranges were well formed. Species of oldest lineages (*E. punctatus* and *E. aureus*) are from the cold temperate zone. From the *E. aureus* ancestor, the ancestor of the *purpurans* group evolved. This ancestor spread to, or was in, Beringia by the Middle Miocene, but cold conditions during the late Miocene divided the ancestral stock. The nearctic stock gave rise to extant *E. purpurans*. The Palaearctic stock gave rise to the common ancestor of *E. ulrichi* and *E. angusticollis*. This last species spread and divided into eastern and western Palaearctic populations which gave rise to two subspecies. The eastern Palaearctic subspecies invaded the western Nearctic region during the Late Pleistocene.

## Conclusion

Beringia was a most important area during the formation of the flora (Wolfe, 1972) and fauna (Simpson, 1953) of the Palaearctic and Nearctic region. This bridge was in existence during most of the Cenozoic period. The main floral and faunal source areas during the first half of this period were either in tropical or temperate Asia (Wolfe, 1972). In Late Tertiary,

North America served also as a source area (Wolfe, 1972; Simpson, 1953). Beringia served mostly as a corridor or filter route for plants and animals adapted to climatic conditions of the bridge. From the Paleocene until the Oligocene, subtropical and paratropical conditions in Alaska allowed tropical Asiatic elements to invade North America. Among carabids I do not know of taxa that use this early route. From the Middle Oligocene until the Early Miocene, numerous temperate Asiatic elements extended into North America. This exchange was extensive, as today numerous extant genera and subgenera are still shared. The following carabid genera used this route then: *Loricera* (Ball and Erwin, 1969), *Badister*, *Diplocheila*, and *Dicaelus* (Ball, 1959), *Calathus* (Ball and Nère, 1972) and *Dicheirus* (Noonan, 1975). During the Late Miocene and the early Pliocene, boreal elements from both continents were exchanged. These elements were derived mostly from temperate counterparts on each continent. Finally, Beringia was the seat of exchange of subarctic and arctic elements during glacial phases of the Pleistocene as suggested by numerous holarctic species of plants and animals shared today (Hultén, 1968; Lindroth, 1961; Ball, 1966) and confirmed by unchanged Pleistocene fossils observed by Lindroth (1969), Coope, (1970) Matthews (1970, 1974a and 1974b) and myself.

In summary, ancestral and extant members of *Elaphrus* crossed Beringia several times. The sole member of *Arctelaphrus* invaded North America during one of the glacial periods of the Pleistocene. In *Neoelaphrus*, one early invasion from Asia occurred in the Late Oligocene followed by another in the Middle Miocene from North America. In *Elaphrus*, one invasion, from North America in the Early Miocene by one or two ancestral species was followed by invasion into North America by two Palaearctic descendants during a glacial period of the Pleistocene. In *Elaphroterus*, one stock invaded North America in the Middle Miocene and another during one of the glacial periods of the Pleistocene.

The ancestral habitat of *Elaphrus* consists of sun-exposed, moist or wet, and open surfaces which are without, with scattered, or dense and short vegetation. This type of habitat is common to adults of some species (usually early lineages) in all subgenera except those of *Elaphroterus*. From this type of habitat, shifts took place in many directions (Fig. 179). In species of *Neoelaphrus*, there were shifts to shaded surfaces (*E. japonicus*, *E. cupreus*, *E. cicatricosus*, *E. lindrothi*, *E. clairvillei* and *E. laevigatus*), to slow moving waters (*E. cupreus*, *E. cicatricosus* and *E. lindrothi*), and to inorganic substrates (*E. lindrothi*). In species of *Elaphrus*, there were shifts to slow moving waters (*E. ruscarius*, *E. californicus*, *E. americanus*, *E. finitimus*, *E. riparius* and *E. tuberculatus*), to inorganic substrates (*E. ruscarius*, *E. californicus*, *E. lecontei*, *E. americanus sylvanus*, *E. finitimus*, *E. riparius*, *E. tuberculatus* and *E. parviceps*), and to saline substrates (*E. lecontei* and *E. lheritieri*). In species of *Elaphroterus*, there were shifts to fast moving waters (all species), to upper beach (all species), and to shaded surfaces (*E. purpurans* and *E. angusticollis longicollis*).

The postulated complex history of elaphrines, with exchanges between continents and distributional changes is best interpreted considering geological and climatic events, but radiations and extant distribution patterns are perhaps best suggested by Wilson's (1961) principle of taxon cycle. The potential of Wilson's theory in biogeography is more concretely illustrated by Wolfe's (1972) study of the origin of the mixed mesophytic and northern hardwood forests. Most elements of these forests originated in older and larger areas with high diversity (farther south), followed by various degrees of radiation in new or younger life zones, but rarely followed by a reciprocal invasion and radiation from northern areas into the more diverse southern communities. I feel students of biogeography of temperate, boreal and arctic

faunas and floras would have much to gain in considering Wilson's theory following an analysis of taxa distribution and their reconstructed phylogeny. Many insects are closely associated with floras similar to those studied by Wolfe, and the pattern suggested by these floras is likely to be similar in those insects. The theory of taxon cycles may have wide application in studies of northern biogeography.

### CONCLUDING REMARKS

What is the future in studies of *Elaphrus*? Systematic and taxonomic problems in need of studies have been outlined along the text and in related publications. Since species of *Elaphrus* are in a mature level of taxonomic and systematic understanding, students in other fields of biological sciences may look upon them as subjects for investigation. Bauer (1973, 1974 and 1976) studied many aspects of the ecology and ethology of species of his region. Some species are stenotopic and others eurytopic, yet we do not know about the stimuli that orient adults to their specific macro- and micro-habitat. The numerous species of *Elaphrus* are likely to be a gold mine of challenges for comparative ethological studies. Firstly, adults are exceptionally easy to observe. Adults of all species are diurnal, active during best weather conditions, and exhibit an exceptionally long period (three to six months) of activity and reproduction, those of most species are on surfaces almost free of vegetation and rough organic debris, and those of many species are restricted narrowly laid habitats. Secondly, there is a wide range of behavior patterns associated with cryptic coloration (displacement, mating, hunting for mates and food, grooming, etc), with type of water in proximity (river or marsh), and with acute sight (mating, hunting for food and mates, enemies etc.).

### ACKNOWLEDGEMENTS

I greatly appreciate G.E. Ball, sponsor of my graduate program, for his continued enthusiasm, encouragement and guidance. I thank all curators and collectors listed in "Materials" for loans of material. I had the privilege of studying types in the care of P.J. Darlington, Jr. (Museum of comparative Zoology, Cambridge, Massachusetts), T.L. Erwin (United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.), D.H. Kavanaugh (California Academy of Science, San Francisco) and C. Jeanne (Bordeaux, France). I thank the above and following gentlemen for numerous courtesies extended during my visits to their respective establishments: D.R. Whitehead, R.T. Bell, W. Rosenberg, N.M. Downie, R.T. Allen, and T.C. Barr. I much appreciate O.L. Kryzhanovskij who kindly checked Semenov's types and tested my work with Palaearctic species, and T. Bauer and R. Davidson who reared and gave me larvae of some species of *Elaphrus*.

I am greatly indebted to E.E. Lindquist, A. Smetana, E.C. Becker and D.M. Wood for many helpful suggestions in editing and for significantly improving the presentation of the text. I also express my gratitude to G.E. Ball, F.E. Goulet, D. Watler, C.D. Dondale and A. Borkent for their comments on parts of the text. I appreciate very much the many enjoyable hours spent discussing taxonomy, evolution, zoogeography and ecology with G.E. Ball, D.H. Kavanaugh, D.R. Whitehead, H.E. Frania, J.S. Ashe, A. Borkent, E.M. Pike, D.M. Wood, W.G. Evans and J.M. Campbell. I also thank H.E. Frania and D.H. Kavanaugh, my field companions during expeditions.

I wish to thank the following friends and colleagues for helping to translate papers of many languages: L. Forester, G.C.D. Griffiths, M. Kimura, L. Masner, A. Smetana and C.M. Yoshimoto. Special thanks and appreciation are extended to a very special person, my wife, Fawn. She went out of her way to encourage and help me in so many ways.

Financial assistance is acknowledged from the following sources: The National Research Council of Canada grant A1399 held by G.E. Ball, and the Boreal Institute (University of Alberta). I very much appreciated air transportation to and from Inuvik, Northwest Territories, arranged by L.C. Bliss (Department of Botany, University of Alberta) through Gulf Oil of Canada Limited. Finally, I thank Richard Hill for providing facilities at the Arctic Research Laboratory, Inuvik, during my visit there in the summer of 1974.

#### LITERATURE CITED

- Allen, R.T. and G.E. Ball. 1979. Synopsis of Mexican taxa of the *Loxandrus* series (Coleoptera: Carabidae: Pterostichini). Transactions of the American Entomological Society 105(4):481-575.
- Antoine, M. 1920. Dix variétés ou aberrations de carabiques nouvelles ou non signalées en France. Miscellanea Entomologica 25:9-12.
- Antoine, M. 1947. Notes d'entomologie marocaine XLV - Découverte du genre *Elaphrus* au Maroc. Bulletin de la Société Entomologique de France 52:26-27.
- Antoine, M. 1955. Coléoptères carabiques du Maroc. Mémoire de la Société des Sciences Naturelles et Physiques du Maroc. I. 170 pp.
- Arnett, R.H., Jr. 1969. Directory of Coleoptera collections of North America (Canada through Panama). Purdue University, Indiana. 123 pp.
- Ashlock, P.D. 1975. The uses of cladistics. Annual Review of Ecology and Systematics 5:81-99.
- Atchley, W.R., C.T. Gaskin and D. Anderson. 1976. Statistical properties of ratios. I. Empirical results. Systematic Zoology 25:138-148.
- Austin, E.P. 1880. Supplement to the check list of the Coleoptera of America North of Mexico. Boston. 67 pp.
- Ball, G.E. 1956. Notes on the genus *Zacotus* LeConte, 1869, and on the classification of the tribe Broscini, (Broscidae sensu Jeannel, 1941. Coleoptera, Carabidae). The Coleopterists Bulletin 10(3):33-52.
- Ball, G.E. 1959. A taxonomic study of the North American Licinini with notes on old world species of the genus *Diplocheila* Brullé (Coleoptera). Memoirs of the American Entomological Society 16:1-258.
- Ball, G.E. 1960. Carabidae. In R.H. Arnett: The beetles of the United States (a manual for identification). The Catholic University of America Press, Washington, D.C. pp. 55-182.
- Ball, G.E. 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). Opuscula Entomologica, Lund, Supplementum 28:1-166.
- Ball, G.E. 1969. The species of the subgenus *Cryobius* of the Kodiak Archipelago. (*Pterostichus*, Carabidae, Coleoptera). In T.N.V. Karlstrom and G.E. Ball (editors): The Kodiak Island refugium: its geology, flora, fauna and history. Ryerson Press, Toronto. pp. 156-194.



- Ball, G.E. 1975. Pericaline Lebiini: Notes on classification, a synopsis of the New World genera and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). *Quaestiones Entomologicae* 11:143–242.
- Ball, G.E. and T.L. Erwin, 1969. A taxonomic synopsis of the tribe Loricerini (Coleoptera: Carabidae). *The Canadian Journal of Zoology*. 47(5):877–907.
- Ball, G.E. and J. Nègre. 1972. The taxonomy of the Nearctic species of the genus *Calathus* Bonelli (Coleoptera: Carabidae: Agonini). *Transactions of the American Entomological Society* 98:412–533.
- Bänninger, M. 1919. Dritter Beitrag zur Kenntnis der Carabinae. Gattungen *Omophron* und *Elaphrus*. *Archiv für Naturgeschichte* 83, A7: 143–150.
- Bänninger, M. 1931. Über Carabinae, Ergänzungen und Berichtigungen. (Col.). Beitrag 17. *Deutsche Entomologische Zeitschrift* 4:177–212.
- Bates, H.W. 1883. Supplement to geodephagous Coleoptera of Japan. *Transactions of the Entomological Society of London*: 205–290.
- Bauer, T. 1973. Stridulation in ground beetles of the genus *Elaphrus* Fabr. (Carabidae). *Forma et Functio* 6:177–190.
- Bauer, T. 1974. Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). *Oecologia* 14:139–196.
- Bauer, T. 1976. Experimente zur Frage der biologischen Bedeutung der Stridulations-verhaltens von Käfern. *Zoologische Tier-Psychologie* 42:56–65.
- Bedel, L.E.M. 1881. Faune des Coléoptères du bassin de la Seine (et de ses bassin secondaires). Vol. I. Appendice aux Annales de la Société Entomologique de France. XXIV 360.
- Bell, R.T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). *Annals of the Entomological Society of America* 60(1):101–107.
- Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or Beetles (exclusive of Rhyncophora) known to occur in Indiana. The Nature Publishing Co., Indianapolis. 1836 pp.
- Bonelli, F.A. 1810. Observations Entomologiques 1. Mémoire della Reale Accademia della Scienze di Torino, 18:21–78.
- Brullé, A. 1834. In Brullé, A. and V. Audouin: Histoire Naturelle des Insectes 4. Coléoptères. VIII+479 pp.
- Casey, T.L. 1897. Coleopterological notices. VII. *Annals of the New York Academy of Sciences* 9:287–684.
- Casey, T.L. 1920. *Memoirs on the Coleoptera* 9:1–529.
- Casey, T.L. 1924. *Memoirs on the Coleoptera* 11:1–347.
- Chaudoir, M. de. 1842. Catalogue des Carabiques recueillis dans la province Mazadéran près d'Astrabat par M. de Karéline. *Bulletin de la Société Impériale des Naturalistes de Moscou* 15(4):801–831.
- Chaudoir, M. de. 1850. Supplément à la faune des Carabiques de la Russie. *Bulletin de la Société Impériale des Naturalistes de Moscou* 23(2):62–206.
- Clark, M.E. 1948. An annotated list of Coleoptera taken at or near Terrace, British Columbia. Part I. *Entomological Society of British Columbia, Proceedings* 44:24–27.
- Coope, G.R. 1970. Interpretation of Quaternary insect fossils. *Annual Review of Entomology* 15:97–120.
- Crotch, G.R. 1873. Check list of the Coleoptera of America, north of Mexico. Salem. 136 pp.

- Crotch, G.R. 1876. *In*: G.H. Horn. Synoptic tables of some genera of Coleoptera with notes and synonymy. Transactions of the American Entomological Society 5:246–252.
- Curtis, J. 1827. British Entomology. Vol. IV. London. Plates 147–194.
- Csiki, E. 1927. Carabidae I. Carabinae II. *In* Junk-Schenkling: Coleopterorum Catalogus, pars 92. Berlin. pp. 315–622.
- Dalla-Torre, K.W. von. 1877. Synopsis der Insecten Oberösterreichs. Jahresbericht des Vereins für Naturkunde Linz 8:15–74.
- Darlington, P.J., Jr. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. Ecological Monographs 13:37–61.
- Darlington, P.J., Jr. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc., New York. 675 pp.
- Darlington, P.J., Jr. 1971. The carabid beetles of New Guinea Part IV. General considerations; analysis and history of fauna; taxonomic supplement. Bulletin of the Museum of Comparative Zoology 142(2):129–337.
- De Geer, C. 1774. Mémoires pour servir à l'histoire des insectes. Stockholm. XII+456 pp.
- Dejean, P.F.M.A. 1826, 1831. Species général des Coléoptères de la collection de M. LeConte Dejean. Méquignon-Marvis, Paris. 2:VIII+501 pp.; 5:VIII+883 pp.
- Dejean, P.F.M.A. and M.J.A. Boisduval. 1830. Iconographie et histoire naturelle des Coléoptères d'Europe. Méquignon-Marvis, Paris. 2: 407 pp.
- Dietz, R.S. and J.C. Holden. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, Permian to Present. Journal of Geophysical Research. 75(26):4939–4956.
- Duftschnid, C. 1812. Fauna Austriae. Vol. 2:311 pp.
- Ekis, G. 1977. Classification, phylogeny and zoogeography of the checkered beetle genus *Perilypus* (Coleoptera: Cleridae). Smithsonian Contributions to Zoology 27:1–138.
- Emden, F.I. van. 1919. Versucheiner Aufstellung von Gattungs bestimmungstabellen der Carabidenlarven (Coleoptera). Supplementa Entomologica. 8:1–33.
- Emden, F.I. van. 1942. A key to the genera of larval Carabidae. Transactions of the Royal Entomological Society 92:1–99.
- Erichson, W.F. 1837. Die Käfer der Mark Brandenburg. I. Berlin. VIII+384 pp.
- Erwin, T.L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). Quaestiones Entomologicae 6:4–215.
- Erwin, T.L. 1978. The larva of Neotropical *Enceladus gigas* Bonelli (Coleoptera: Carabidae: Siagoninae: Enceladini) with notes on the phylogeny and classification of some of the more primitive tribes of ground beetles. The Coleopterists Bulletin 32:99–106.
- Erwin, T.L. 1979. Thoughts on evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. *In* T.L. Erwin, G.E. Ball, D.R. Whitehead and A.L. Halpern (Editors): Carabid beetles: their evolution, natural history, and classification. Dr. W. Junk, The Hague - Boston-London. pp. 539–592.
- Everts, E.J.G. 1898. Coleoptera Neerlandica. De schildvleugelige insecten van Nederland en het aangrenzend gebied. Vol. I.'s Gravenhage. VIII+676 pp.
- Fabricius, J.C. 1775. Systema Entomologiae. Flensburgi et Lipsiae. 30+832 pp.
- Fabricius, J.C. 1792. Entomologiae Systematicae. Vol. I. Hafniae, pars 1:20+330 pp.; pars 2:538 pp.
- Fabricius, J.C. 1801. Systema Eleutheratorum. Vol. I (1). Kiliae. XXIV 506 pp.

- Fairmaire, L. 1913. Histoire naturelle de la France, 8 ième partie Coléoptères. Deyrolle, Paris. III + 505 pp.
- Fairmaire, L. and A. Laboulbène. 1854. Faune entomologique française. I. Deyrolles, Paris. 665 pp.
- Fauvel, A. 1882. Faune Gallo-Rhénane, ou species des insectes qui habitent la France, la Belgique, la Hollande, le Luxembourg, la Prusse Rhénane, le Nassau et le Valais. II. 220 pp.
- Fischer von Waldheim, G. 1828. Entomographia imperii Russici... (Entomographie de la Russie ...). Vol. 3. Mosquae. 8 + 314 pp.
- Fischer von Waldeim, G. 1829. In: B. Zoubkoff: Notice sur un nouveau genre et quelques nouvelles espèces de Coléoptères. Bulletin de la Société Impériale des Naturalistes de Moscou I:147–168.
- Forsythe, T.G. 1978. Preliminary investigation into the stridulation mechanisms of the genus *Elaphrus* (Coleoptera: Carabidae): *Elaphrus cupreus* Duftschmid. The Coleopterists Bulletin 32(1):41–46.
- Freude, H. 1976. In H. Freude K.W. Harde and G.A. Lohse: Die Käfer Mitteleuropas. Band 2. Goecke and Evers, Krefeld. 302 pp.
- Frost, C.A. 1910. Ethological notes on *Elaphrus cicatricosus* LeConte (Coleoptera). Psyche 17:256–257.
- Gahan, J. 1900. X. Stridulating organs in Coleoptera. Transactions of the Entomological Society of London: 433–452.
- Ganglbauer, L. 1892. Die Käfer von Mitteleuropa. I. Wien. III + 557 pp.
- Gaubil, J. 1849. Catalogue synonymique des Coléoptères d'Europe et d'Algérie. Paris. 297 pp.
- Geoffroy, E.L. 1799. Histoire abrégée des insectes.... Vol. I (new edition) Paris. XXVIII + 556 pp.
- Gerhardt, J. 1899. Neuheiten der Schlesischen Käferfauna aus dem Jahre 1898. Zeitschrift für Entomologie Breslau, N.F. 24:14–19.
- Goulet, H. 1964. Etude écologique de l'*Elaphrus californicus* Man. Travaux des Jeunes Scientifiques 1(1):77–96; 1(2):97–103.
- Goulet, H. 1976. A method for rearing ground beetles (Coleoptera: Carabidae). The Coleopterists Bulletin 30(1):33–36.
- Goulet, H., and B.R. Baum. 1981. Analysis of variation in the *Elaphrus americanus* complex of North America (Coleoptera: Carabidae). Canadian Journal of Zoology 59(12):2253–2274.
- Goulet, H., and B.R. Baum. 1982. Analysis of variation in the *Elaphrus finitimus* complex of North America (Coleoptera: Carabidae). Canadian Journal of Zoology 60(10):2424–2433.
- Goulet, H., and A. Smetana. 1983. A new species of *Blethisa* Bonelli from Alaska, with proposed phylogeny, biogeographic history, and key to known species (Coleoptera: Carabidae). The Canadian Entomologist 115:551–558.
- Guppy, R. 1947. Some records of Carabidae collected on Vancouver Island with ecological data. The Coleopterists Bulletin 1:51–52.
- Guppy, R. 1948. Correction and additions to "Some records of Carabidae collected on Vancouver Island (The Coleopterists Bulletin 1:51–52, 1947)". The Coleopterists Bulletin 2:75–76.
- Gyllenhal, L. 1810, 1827. Insecta Suecica descripta. Vol. I(2): XX + 660 pp., Scaris. Vol. I(4),

Lipsiae. XI+760 pp.

- Habu, A. 1953. Shin Konchû 6(4): 19. (Not seen; cited by Uéno, 1954: 718).
- Habu, A. 1961. Revisional study of the species of the Trichotichni, the subtribe Harpalini from Japan (Coleoptera, Carabidae). Bulletin of National Institute of Agricultural Sciences, (C) 13:127-169.
- Harrington, W.H. 1889. On the lists of Coleoptera published by the Geological Survey of Canada 1842-1888. The Canadian Entomologist 11:135-140.
- Hatch, M.H. 1951. Studies on the Coleoptera of the Pacific Northwest. IV. Carabidae, Dytiscidae, Gyrinidae. Bulletin of the Brooklyn Entomological Society 46:113-122.
- Hatch, M.H. 1953. The beetles of the Pacific Northwest. I. University of Washington Press, Seattle. VII+340 pp.
- Hausen, J.F. 1891. Aids to the study of Canadian Coleoptera. Canadian Record of Science 4(5):251-255.
- Heer, O. 1838. Fauna Coleopterorum Helvetica. I. Turici, Orellii etc. 12+652 pp.
- Hecht, M.K. and J.L. Edwards. 1977. The methodology of phylogenetic inference above the species level. In M.K. Hecht, P.C. Goody and B.M. Hecht (Editors): Major patterns in vertebrate evolution. NATO Advanced Study Institute. Series A. Vol. 14:3-51.
- Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana. 263 pp.
- Hippisley, M.E. (Mrs. W.W. Clark). 1922. Notes on northern British Columbia Coleoptera. The Canadian Entomologist 54:63-66.
- Hlavac, T.F. 1971. Differentiation of the carabid antennal cleaner. Psyche 78:51-66.
- Hopkins, D.M. 1967. The Cenozoic history of Beringia - a synthesis. In D.M. Hopkins (Editor): The Bering Land Bridge. Stanford University Press, Stanford, California. pp. 451-484.
- Horn, G.H. 1878. Contributions to the coleopterology of the United States. No. 2. Transactions of the American Entomological Society 7:51-60.
- Horn, G.H. 1881. On the genera of Carabidae with special reference to the fauna of boreal America. Transactions of the American Entomological Society 9:91-196.
- Hultén, E. 1968. Flora of Alaska and neighboring territories. A manual of the vascular plants. Stanford University Press, Stanford. VII+1008 pp.
- Illiger, J.K.W. 1798. Verzeichnis der Käfer Preussens. Vol. 1 Gebauer, Halle. XLII+510 pp.
- Jacobson, G.G. 1906. Zhuki Rossii i zapadnoy Evropy. St. Petersburg. II fasc. 1024 pp.
- Jacobson, G.G. 1931. Opredeliteli Zhukov. Prakticheskaya Entomologia. 472 pp.
- Jacquelin du Val, P.N.C. 1857. Genera des Coléoptères d'Europe. I. Paris. 4+CCXXVI+140 pp.
- Jeanne, C. 1966. Carabiques de la péninsule Ibérique (3ième note). Actes de la Société Linnéenne de Bordeaux 103:3-18.
- Jeannel, R. 1941. Faune de France 39. Coléoptères Carabiques. Partie 1. Paris. 571 pp.
- Jeannel, R. 1942. La genèse des Faunes terrestres. Eléments de biogéographie. Presses universitaires de France, Paris. VIII+513 pp.
- Joy, N.H. 1932. A practical handbook of British Beetles. I. London. XXVII+622 pp.
- Judd, W.W. 1967. Insects from McConnell River, NWT. Entomological News 78(2):50-55.
- Kavanaugh, D.H. 1972. Hennig's principles and methods of phylogenetic systematics. The Biologist 54(3):115-127.
- Kavanaugh, D.H. 1978. Hennig phylogenetics in contemporary systematics: principles, methods and uses. In: Beltsville Symposia in Agriculture, 2. Biosystematics in

- agriculture. Allenheld, Osmen and Co., Montclair, N.J. pp. 139–150.
- Keen, J.H. 1905. Beetles from northern British Columbia. The Canadian Entomologist 37:297–298.
- Kirby, W. 1837. The insects. In J. Richardson: Fauna boreali-americana;...Part 4. 325 pp.
- Kuhnt, P. 1912. Illustrierte Bestimmungstabellen der Käfer Deutschlands. Stuttgart. VII+3+1138 pp.
- Küster, H.C. 1846. Die Käfer Europas. Part VII. Nurnberg.
- Kuster, J.E. 1979. Comparative structure of compound eyes of Cicindelidae and Carabidae (Coleoptera): evolution of scotopy and photopy. Quaestiones Entomologicae 15:297–334.
- Lacordaire, M. Th. 1854. Histoire naturelle des insectes. Genera des Coléoptères. Tome 1. Roret, Paris. XX+486 pp.
- La Rivers, I. 1946. An annotated list of Carabinae known to occur in Nevada (Coleoptera: Carabidae). Bulletin of the Southern California Academy of Sciences 45:133–140.
- Larochelle, A. 1975. Les Carabidae du Québec et du Labrador. Département de Biologie du Collège Bourget, Rigaud. 225 pp.
- Latreille, P.A. 1796. Précis des caractères génériques des insectes disposés dans un ordre naturel. Brive, Bordeaux. 14+201+7 pp.
- Latreille, P.A. 1802, 1804. Histoire naturelle générale et particulière des Crustacés et des Insectes. Paris. II:XII+467 pp.; VIII+411 pp.
- Latreille, P.A. 1806. Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Vol I. Paris. XVIII+302 pp.
- Latreille, P.A. 1810. Considérations générales sur l'ordre naturel des animaux. Paris. 444 pp.
- Leach, W.E. 1815. Entomology. In Brewster: Edinburgh Encyclopaedia. Vol. 9 Edinburgh. pp. 57–172.
- LeConte, J.L. 1848. A descriptive catalogue of the Geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York 4:173–474 (pp. 234–333 omitted by a mistake of the printer).
- LeConte, J.L. 1850. General remarks upon the Coleoptera of Lake Superior. In J.L.L. Agassiz: Lake Superior 4:201–242.
- Leconte, J.L. 1852. Description of new species of Coleoptera, from California. Annals of the Lyceum of Natural History of New York 5:185–216.
- LeConte, J.L. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society, Philadelphia 10:363–403.
- LeConte, J.L. 1861. Classification of Coleoptera of North America. I. Smithsonian Miscellaneous Collections 3:XXV+286 pp.
- LeConte, J.L. 1863. New species of North American Coleoptera. I. Smithsonian Miscellaneous Collections 6(167):1–86.
- LeConte, J.L., and G.H. Horn. 1883. Classification of the Coleoptera of North America. Second edition. Smithsonian Miscellaneous Collections, XXXVIII+567 pp.
- Leng, C.W. 1918. Notes on some changes in the list of Coleoptera. Journal of the New York Entomological Society 26:201–211.
- Letzner, K. 1849. Systematische Beschreibung der Laufkäfer Schlesiens. Zeitschrift für Entomologie Breslau 10(2):21–52.
- Lindroth, C.H. 1939. Zur Systematik fennoskandischer Carabiden 2-3. 3. Über *Elaphrus*

- tuberculatus* Mäklin (*latipennis* J. Shalberg, *tumidiceps* Munster). Entomologisk Tidskrift 60:62–68.
- Lindroth, C.H. 1945, 1949. Die fennoskandischen Carabidae. I-III Göteborgs Kungliga Vetenskap och Vitterhets-Samhälles Handlingar (6) B. 4.I: 1–709; II: 1–277; III: 1–911.
- Lindroth, C.H. 1954. A revision of *Diacheila* Motschulsky and *Blethisa* Bonelli with remarks on *Elaphrus* larvae (Col.: Carabidae). Kungliga Fysiografiska Sällskapets Handlingar (N.F.) 65:1–28.
- Lindroth, C.H. 1955. The carabid beetles of Newfoundland. Opuscula Entomologica, Lund, Supplementum 12:1–160.
- Lindroth, C.H. 1957. The Linnaean species of carabid beetles. Journal of the Linnean Society-Zoology 43: 325–341.
- Lindroth, C.H. 1961, 1969a. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Opuscula Entomologica, Lund, Supplementum 20:1-200;35:I–XLVIII.
- Lindroth, C.H. 1969b. An analysis of the carabid beetle fauna of the refugium. In T.N.V. Karlstrom and G.E. Ball (editors): The Kodiak Island refugium: its geology, flora, fauna and history. Ryerson Press, Toronto. pp. 145–215.
- Lindroth, C.H. 1974. Handbook for the identification of British insects. Coleoptera, Carabidae. Royal Entomological Society of London 4(2):1-148.
- Lindroth, C.H. 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. The Coleopterists Bulletin 29(2):109–147.
- Lindroth, C.H. and R. Freitag. 1969. North American ground-beetles (Coleopt. Carabidae, excl. Cicindelinae) described by Thomas Say. Designation of lectotypes and neotypes. Psyche 76:328–361.
- Linnaeus, C. 1758. Systema naturae. X. Vol. I. L. Salvii, Holmiae. 3+824 pp.
- Louvet, G. 1925. Etude morphologique de l'*Elaphrus uliginosus* et de ses variétés. Description d'une aberration nouvelle. Miscellanea Entomologica 29(2):17–20.
- Luff, M.L. 1976. The larvae of the British Carabidae (Coleoptera). IV Notiophilini and Elaphrini. Entomologist's Gazette 27:51–67.
- Mäklin, F.W. 1877. Diagnos öfver några nya sibiriska insektarter. Öfversigt af Finska Vetenskaps-Societetens Förhandlingar 19:10–17 (pages seen).
- Mannerheim, C.G. 1843. Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sithka and New Californiens. Bulletin de la Société Impériale des Naturalistes de Moscou 16(2):175–314.
- Mannerheim, C.G. 1853. Dritter Nachtrag zur Kaefer-Fauna der Nord-Amerikanischen Laender des Russichen Reiches. Bulletin de la Société Impériale des Naturalistes de Moscou. 26(3):95–273.
- Marseul, M.S.A. 1880. Nouveau répertoire contenant les descriptions des espèces des Coléoptères de l'ancien-monde. L'Abeille 19:1–526.
- Marseul, M.S.A. 1882. Catalogue synonymique et géographique des Coléoptères de l'ancien-monde. L'Abeille 20:1–60.
- Matthews, J.V., 1970. Two new species of *Micropeplus* from Pliocene of western Alaska with remarks on the evolution of Micropeplinae (Coleoptera: Staphylinidae). Canadian Journal of Zoology 48: 779-788.
- Matthews, J.V., Jr. 1974a. A preliminary list of insect fossils from the Beaufort Formation,

- Meighen Island, District Franklin, N.W.T. Geological Survey of Canada. Paper 74-1, Part A:203-206.
- Matthews, J.V., 1974b. Fossil insects from early Pleistocene Olyor Suite (Chukochya River: Kolymian Lowland, U.S.S.R.). Geological Survey of Canada. Paper 74-1, Part A. pp. 207-211.
- Matthews, J.V., Jr. 1976. Evolution of the subgenus *Cyphelophorus* (Genus *Helophorus*, Hydrophilidae, Coleoptera): description of two new fossil species and discussion of *Helophorus tuberculatus* Gyll. Canadian Journal of Zoology 54:652-673.
- Matthews, J.V., Jr. 1979. Tertiary and quaternary environments: historical background for an analysis of the Canadian insect fauna. In H.V. Danks (editor): Canada and its insect fauna. Memoirs of the Entomological Society of Canada 108. pp. 31-86.
- Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York. X+328 pp.
- Méquignon, M. 1924. Liste des Coléoptères recueillis à Saclas, par M. Bedel. Annales de la Société Entomologique de France 93:125-160.
- Morawitz, A. 1863. (title not seen). Bulletin de l'Académie des Sciences, St. Petersburg 4:191.
- Motschulsky, T.V. von. 1845. Observations sur le Musée entomologique de l'Université Impériale de Moscou. Bulletin de la Société Impériale des Naturalistes de Moscou 18(4):332-388.
- Motschulsky, T.V. von, 1846. Insectes de la Sibérie. Mémoire de l'Académie des Sciences, St. Petersburg 13:1-274.
- Motschulsky, T.V. von, 1850a. Die Kaefer Russlands. I. Insecta Carabica. Moskva VII+91 pp.
- Motschulsky, T.V. von, 1850b. Séance du 27 novembre 1850. Présidence de M. Chevrolat. (Sur un *Elaphrus* nouveau des Pyrénées et du midi de la France). Annales de la Société Entomologique de France 8(2). Bulletin Entomologique. pp. LXVI-LXVII.
- Müller, O.F. 1764. Fauna insectorum Fridrichsdalina ... Hafniae et Lipsiae. 24+96 pp.
- Müller, O.F. 1776. Zoologiae Danicae prodromus. ... Hafniae. 32+282 pp.
- Müller, P.W.J. 1821. Neue Insecten beschrieben von Müller. Magazin der Entomologie 4:184-230.
- Munster, T. 1924. Nova etc. ex Norvegia. Norsk Entomologisk Tidsskrift 1(6):288-294.
- Nakane, T. 1955. Colored illustrations of insects of Japan. Coleoptera. Osaka. 274 pp.
- Nakane, T., K. Ohbayashi, S. Nomura and Y. Kurosawa. 1963. Iconographia insectorum Japonicorum colore naturali edita. Volumen II (Coleoptera). Tokyo. 443 pp.
- Noonan, G.R. 1973. The anisodactylines (Insecta: Coleoptera: Carabidae: Harpalinae): classification, evolution and zoogeography. Quaestiones Entomologicae 9:266-480.
- Noonan, G.R. 1975. Bionomics, evolution and zoogeography of members of the genus *Dicheirus* (Coleoptera: Carabidae). The Pan-Pacific Entomologist 51(1):1-15.
- Obenberger, J. 1917. Beitrag zur Kenntnis der palaearctischen Käferfauna. Archiv für Naturgeschichte 82, A4:9-10 (pages seen).
- Ohkura, J. 1973. Ground beetles in Japan (3): Paussidae and Carabidae. Nature and Insects 8(11):2-7.
- Olivier, G.A. 1790. Entomologie ou histoire naturelle des insectes Coléoptères II. Paris. 6+485 pp.
- Palmén, E. 1944. Über die Artengruppe *Elaphrus angusticollis* F. Sahlb. (Col., Carabidae). Annales Entomologici Fennici 10:17-25.
- Palmén, E. and S. Platonoff. 1943. Zur Autökologie und verbreitung der ost fennoskandischen Flussuferkäfer. Annales Entomologici Fennici 9:74-144.

- Panzer, G.W.F. 1793. *Faunae Insectorum Germanicae initia, oder Deutschlands Insecten*. 20 Hft. Nürnberg.
- Pierce, W.D. 1948a. Fossil arthropods from British Columbia 4. An *Elaphrus* from interglacial lignite. *Bulletin, Southern California Academy of Sciences* 47(2):52.
- Pierce, W.D. 1948b. Fossil arthropods of California. 16. The carabid genus *Elaphrus* in the asphalt deposits. *Bulletin, Southern California Academy of Sciences* 47(2):53–55.
- Poda von Neuhaus, N. 1761. *Insecta Musei Graecensis ... Graecii*. 127 + 18 pp.
- Poppius, B. 1908. Über einige sibirische und nordwest amerikanische Käfer-Arten. *Öfversight of Finska Vetenskaps-Societetens Förhandlingar* 50(6):1–7.
- Porta, A. 1923. *Fauna Coleopterorum Italica*. I. Piacenza. VI + 2 + 285 pp.
- Portevin, G. 1929. *Histoire naturelle des Coléoptères de France*. I. Paris. X + 649 pp.
- Redtenbacher, W. 1842. *Coleopterorum Archiducatus Austriae nondem descriptorum*. Vindobonae. 31 pp.
- Redtenbacher, L. 1874. *Fauna Austriaca*. Die Käfer nach der analytischen Methode bearbeitet. Ed. 3. Wien. Vol. I:CLIII + 564 pp.; Vol. II:XLIII + 571 pp.
- Reitter, E. 1887. Neue Coleopteren aus Europa, den angrenzenden Ländern und Sibirien, mit Bemerkungen über bekannte Arten. *Deutsche Entomologische Zeitschrift* 31(1):241–288.
- Reitter, E. 1908. *Fauna Germanica*. Die Käfer des Deutschen Reiches I. Stuttgart. 38 + 248 pp.
- Reitter, E. 1909. *Coleoptera* (Heft 3-4). In A. Brauer (Ed): *Die Süßwasserfauna Deutschlands*. Jena. IV + 235 pp.
- Ross, H.H. 1974. *Biological systematics*. Addison-Wesley, Don Mills. 345 pp.
- Rossi, P. 1790. *Fauna Etrusca, sistens Insecta, quae in provinciis Florentina et Pisana praesertim collegit*. I. Luburni. 272 pp.
- Sahlberg, J. 1880. Bidrag till Nordvestra Sibiriens Insektafauna. *Coleoptera*. Kungliga Svenska Vetenskaps-Akademiens Handlingar 17:1–115.
- Sahlberg, R.F. 1844. In *Faunam Insectorum Rossicam symbola, novas ad Ochotsk lectas Carabicornum species sistens*. Helsingfors. 63 pp.
- Say, T. 1823. Description of insects of the families Carabici and Hydrocanthari of Latreille inhabiting North America. *Transactions of the American Philosophical Society*, N. S. 2(1):109.
- Say, T. 1834. Descriptions of new North American insects, and observations on some already described. *Transactions of the American Philosophical Society* 4:409–470.
- Schaufuss, C. 1916. In *Calwer: Käferbuch, Naturgeschichte der Käfer Europas*. Ed. 6. Vol. I. Stuttgart. LIX + 715 pp.
- Schaum, H. 1856. *Coleoptera* I(1). In W.F. Erichson: *Naturgeschichte der Insecten Deutschlands*. Nicolai, Berlin. VI + 791 pp.
- Schaum, H. 1856–1860. *Coleoptera* Erster Band. In Erichson, W.F. *Naturgeschichte der Insecten Deutschlands*. Nicolaische Verlagsbuchhandlung (G. Parthey), Berlin. VI + 791 pp.
- Schaupp, F.G. 1878. Synoptic table of the genus *Elaphrus*. Latr. *Bulletin of the Brooklyn Entomological Society* 1(1):6.
- Schaupp, F.G. 1878. Synoptic table of the Elaphrini. *Bulletin of the Brooklyn Entomological Society* 1(1):29.
- Schilsky, J. 1889. Synonymische und andere Bemerkungen zu Dr. Carl W.v. Dalla Torre's



“Synopsis der Insecten Oberösterreichs” und “Die Käferfauna von Oberösterreich”.  
Deutsche Entomologische Zeitschrift: 345–356.

Schiødte, J.C. 1841. Genera og Species af Danmarks Eleutherata. Vol. I. Kjöbenhavn.  
12+612+22 pp.

Schiødte, J.C. 1867. De metamorphosi Eleutheratorum observationes: Bidrag til insekternes  
udviklingshistorie. Naturhistorisk Tidsskrift (3)4:415–552.

Schrank, F.V.P. 1781. Enumeratio Insectorum Austriae indigenorum. Augustae Vindelicorum.  
22+548 pp.

Scudder, S.H. 1890. The Tertiary insects of North America. Report of the United States  
Geological Survey of the Territories 13:1–734.

Seidlitz, G.C.M. 1875. Fauna Baltica. Die Käfer (Coleoptera) der Ostseeprovinzen Russlands.  
Ed. 1. Dorpat. 2+XLII+142+560 pp.

Seidlitz, G.C.M. 1891. Fauna Transsylvanica. Die Käfer (Coleoptera) Siebenbürgens.  
Königsberg. 56+914 pp.

Semenov, A. 1889. Diagnosis Coleopterorum novorum ex Asia Centrali et Orientali. Horae  
Societatis Entomologicae Rossicae 23:348–403.

Semenov, A. 1895. Coleoptera nova Rossiae Europaeae Caucasique. Horae Societatis  
Entomologicae Rossicae 29:303–327.

Semenov, A. 1897. Coleoptera nova Rossiae Europaeae Caucasique. Horae Societatis  
Entomologicae Rossicae 31:595–602.

Semenov, A. 1904a. Synopsis Elaphrorum Palearcticorum subgeneris Elaphroteri Sem. gregem  
*El. riparii* (L.) efficientium (Coleoptera, Carabidae). Revue Russe d'Entomologie  
4:19–22.

Semenov, A. 1904b. Appendix I. *Elaphrus latipennis*. Horae Societatis Entomologicae  
Rossicae 37:124–125.

Semenov, A. 1904c. Notice critique sur les *Elaphrus jakovlewi* Semenov, *longicollis* J.  
Sahlberg et *angusticollis* F. Sahlberg (Coleoptera, Carabidae). Revue Russe  
d'Entomologie 4:102–105.

Semenov, A. 1907. Analecta coleopterologica. Revue Russe d'Entomologie 7:258–265.

Semenov, A. 1909. Analecta coleopterologica. Revue Russe d'Entomologie 4:433.

Semenov, A. 1926. Analecta coleopterologica. 29. Revue Russe d'Entomologie 20: 31–55.

Sharova, I. Kh. 1958. Lichinki Zhukov-Zhughelits (Carabidae) Poleznykh i Vrednykh v  
Sel'skom Khosyaistve. Uchenye Zapiski Moskovskogo Gosudarstvennogo  
Pedagogicheskogo Instituta Imeni Lenina 124:4–165.

Silfverberg, H. 1977. Nomenclatoric Notes on Coleoptera Adephaga Carabidae. Notulae  
Entomologicae 57:41–44.

Simpson, G.G. 1953. Evolution and Geography. An essay on historical biogeography with  
special reference to mammals. Oregon State System of Higher Education. 64 pp.

Simpson, G.G. 1961. Principles of animal taxonomy. Columbia University Press, New York.  
XII+247 pp.

Sloane, T.G. 1923. The classification of the family Carabidae. Transactions of the  
Entomological Society of London: 234–250.

Smetana, A. 1949. Inventa Carabidarum minus frequentium in RCS. Folia Entomologica  
12:107–109.

Smetana, A. 1951. Additio ad cognitionem faunae Coleopterorum Montium Vysoké Tatry.  
Acta Societatis Entomologicae Czechosloveniae 48:229–238.

- Smetana, A. 1971. Revision of the tribe Quediini of America North of Mexico (Coleoptera: Staphylinidae). *Memoirs of the Entomological Society of Canada* 79: 303 pp.
- Sokal, R.R. and P.H.A. Sneath. 1963. *Principles of numerical taxonomy*. W.H. Freeman, San Francisco. 359 pp.
- Solsky, S. 1872. Coléoptères de la Sibérie orientale. *Horae Societatis Entomologicae Rossicae* 8:232-277.
- Stierlin, G. 1869. *Fauna Coleopterorum Helvetica. Die Käferfauna der Schweiz*. Schaufhausen. 372 pp.
- Tanner, V.M. 1941. A new *Elaphrus* (Coleoptera, Carabidae). *Great Basin Naturalist* 2(4): 137-138.
- Taylor, W.G. 1886. The entomology of Vancouver Island. Notes on twenty-six species of Cicindelidae and Carabidae collected near Victoria, Vancouver Island. *The Canadian Entomologist* 18:34-37.
- Thomson, C.G. 1859. *Skandinaviens Coleoptera, synoptiskt bearbetade*. I. Lund. 2 + 290 pp.
- Turin, H., J. Haeck and R. Hengeveld. 1977. *Atlas of the Carabid beetles of the Netherlands*. North-Holland Publishing Co., Amsterdam. 228 pp.
- Uéno, S.-I. 1953. Shin Knochû 6(4): 51. (Not seen; cited by Uéno, 1954: 718).
- Uéno, S.-I. 1954. A list of adephagous beetles from the Ozegahara Moor, with the description of new species. *Scientific Researches of the Ozegahara Moor*. pp. 718-726.
- Van Dyke, E.C. 1924. The Coleoptera collected by the Katmai expeditions. *National Geographic Society Contributed Technical Papers* 2(1):1-26.
- Van Dyke, E.C. 1925. Studies of western North American Carabinae (Coleoptera) with descriptions of new species. *Pan-Pacific Entomologist* 1:111-125.
- Venables, E.P. 1913. Notes on some Coleoptera of the Okanagan Valley. *The Canadian Entomologist* 45:267-268.
- Wagner, Von H. 1917. Beiträge zur Coleopterenfauna der Mark Brandenburg V. *Entomologische Mitteilungen* 6:259-273.
- Walker, F. 1866. List of Coleoptera. In J.K. Lord: *The naturalist in Vancouver Island and British Columbia*. Vol. II. Bentley, London. pp. 309-334.
- Whitehead, D.R. 1972. Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). *Quaestiones Entomologicae* 8:131-348.
- Wickham, H.F. 1893. Report on entomological reconnoissance of southern Alaska. *Bulletin from the Laboratory of Natural History of the State University of Iowa* 2:202-233.
- Wiley, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27(1):17-26.
- Williams, G.D. and C.R. Stelck. 1975. Speculations on the Cretaceous Palaeogeography of North America. *The Geological Association of Canada. Special paper* 13:1-20.
- Wilson, E.O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95:169-193.
- Wolfe, J.A. 1972. An interpretation of Alaskan tertiary floras. In: A. Graham (Editor), *Floristics and Paleofloristics of Asia and eastern North America*. Elsevier Publishing Co., Amsterdam. pp. 201-233.
- Xamheu, P.J.V. 1898. Moeurs et métamorphoses d'insectes. *Annales de la Société Linnéenne de Lyon*. 45:157-214.
- Xamheu, P.J.V. 1901. Moeurs et métamorphoses des insectes. *Revue d'Entomologie* 20:7-68.
- Zimsen, E. 1964. *The type material of I.C. Fabricius, Munksgaard, Copenhagen*. 656 pp.

Zoubkoff, B. 1829. Notice sur un nouveau genre et quelques nouvelles espèces de Coléoptères.  
Bulletin de la Société Impériale des Naturalistes de Moscou 1: 147–168, 2 planches.

## INDEX TO NAMES OF TAXA

(Synonyms in *italics*)

## FAMILY GROUP TAXA

Ansiodactylina, 459  
 Broscina, 445, 459, 460  
 Broscini, 445  
 Carabidae, 445  
 Caraboidea Limbata, 445  
 Caraboidea Simplicia, 445  
 Cicindelini, 445  
*Elaphri*, 230  
*Elaphridae*, 230  
*Elaphrides*, 230  
*Elaphrii*, 230  
*Elaphrina*, 230  
*Elaphrinae*, 230  
 Elaphrini, 232, 266, 379, 445, 447, 451,  
     452, 458, 459, 460  
*Elaphrites*, 230  
 Isopleuri, 445  
 Loricerini, 445  
 Melaenini, 445, 459, 460  
 Migadopini, 445  
 Nomiini, 445  
 Patrobini, 445  
 Scaritini, 445  
 Scrobifera, 445  
 Stylifera, 445  
  
 GENERA AND SUBGENERA  
 Arctelaphrus Semenov, 240, 241, 376,  
     378, 379, 380, 447, 452, 462, 464  
*Arctobia* Thomson, 235  
 Bembidion Latreille, 221  
 Blethisa Bonelli, 221, 232, 233, 234, 236,  
     376, 378, 379, 380, 381, 447, 452, 455,  
     457, 459, 460, 461  
 Diacheila Motschulsky, 232, 233, 234,  
     235, 237, 376, 378, 379, 380, 445, 447,  
     452, 455, 457, 459, 460, 461  
*Diachila* Motschulsky, 235  
*Elaphrotatus* Semenov, 322, 378  
 Elaphroterus Semenov, 240, 241, 322, 333,  
     376, 379, 447, 452, 457, 459, 463, 464  
 Elaphrus Fabricius, 221, 225, 227, 229,

232, 233, 234, 238, 241, 246, 257, 282,  
 376, 378, 379, 380, 381, 447, 451, 452,  
 455, 456, 457, 459, 460, 461, 464, 465  
*Elaphrus sensu stricto*, 321, 322, 376, 378,  
     379, 447, 448, 452, 457, 458, 460  
*Helobium* Leach, 236  
 Neoelaphrus Hatch, 240, 241, 246, 259,  
     376, 378, 379, 447, 452, 457, 459, 460,  
     462, 464  
 Notiophilus Duméril, 221  
 Opisthius Kirby, 221  
 Pelophila Dejean, 221  
*Rhaphiona* Fisher von Waldheim, 236

## SPECIES AND SUBSPECIES

americanus Dejean, *Elaphrus*, 268, 271,  
     285, 287, 288, 289, 299, 303, 304, 306,  
     307, 318, 320, 321, 322, 375, 451, 457,  
     463, 464  
 americanus Dejean, *Elaphrus americanus*,  
     307, 310, 311  
*angustatus* Chaudoir, *Elaphrus*, 334, 336  
*angusticollis* Sahlberg, *Elaphrus*, 334, 375,  
     376, 451, 463  
*angusticollis* Sahlberg, *Elaphrus*  
     *angusticollis*, 324, 325, 326, 334, 336,  
     337, 375, 458  
*arctica* Gyllenhal, *Diacheila*, 236, 456, 459  
*arcticus* Dejean, *Elaphrus cupreus*, 268  
*arcticus* Gyllenhal, *Harpalus*, 235  
*atratus* Wagner, *Elaphrus riparius*, 314  
*aureus* Müller, *Elaphrus*, 226, 322, 323,  
     324, 325, 328, 330, 332, 375, 463  
*austriacus* Ulrich, *Elaphrus*, 338  
*baraneki* Semenov, *Elaphrus*, 338  
*baschkiricus* Motschulsky, *Elaphrus*, 313,  
     315  
*bedeli* Méquignon, *Elaphrus*, 255, 257  
*beraneki* Reitter, *Elaphrus*, 338, 340  
*bituberosus* Casey, *Elaphrus*, 307  
*borealis* Andersch, *Elaphrus*, 268  
*californicus* Mannerheim, *Elaphrus*, 285,  
     286, 287, 288, 289, 293, 297, 299, 306,

- 307, 309, 311, 321, 375, 451, 457, 463, 464  
*caseyi* Leng, *Elaphrus*, 280  
*cicatricosus* LeConte, *Elaphrus*, 249, 250, 251, 253, 260, 262, 264, 276, 280, 375, 448, 464  
*clairvillei* Kirby, *Elaphrus*, 249, 251, 252, 253, 262, 264, 267, 268, 270, 271, 275, 280, 282, 334, 375, 457, 458, 460, 463, 464  
*comatus* n. sp., *Elaphrus*, 286, 293, 311, 314, 315, 316, 451  
*costulatus* Uéno, *Elaphrus jakovlewi*, 336  
*costulifer* Semenov, *Elaphrus latipennis*, 316  
*costulifer* Semenov, *Elaphrus tuberculatus*, 316  
*cribratus* Semenov, *Elaphrus*, 326, 327  
*cupreus* Duftschmid, *Elaphrus*, 226, 249, 250, 252, 254, 257, 258, 268, 271, 275, 376, 460, 462, 464  
*cupreus* Habu, *Elaphrus*, 254, 448  
*cupritarsis* Bänninger, *Elaphrus riparius*, 314  
*dauricus* Morawitz, *Elaphrus*, 268  
*dauricus* Morawitz, *Elaphrus cupreus*, 268  
*dilaticollis* Sahlberg, *Elaphrus*, 313, 315, 318, 320  
*divinctus* Casey, *Elaphrus*, 295, 298  
*elongatus* Fischer von Waldheim, *Elaphrus*, 242  
*elongatus* Fischer von Waldheim, *Elaphrus lapponicus*, 242  
*eschscholtzi* Zoubkoff, Blethisa, 236, 457  
*fausti* Heyden, Diacheila, 236  
*finitimus* Casey, *Elaphrus*, 285, 288, 289, 291, 293, 299, 303, 304, 306, 307, 309, 311, 375, 451, 463, 464  
*fluviatile* Linnaeus, Equisetum, 336  
*frosti* Hippiusley, *Elaphrus*, 271  
*frosti* Hippiusley, *Elaphrus clairvillei*, 271  
*fuliginosus* Say, *Elaphrus*, 240, 248, 250, 251, 253, 258, 260, 264, 276, 375, 458, 460  
*gratiosus* Mannerheim, *Elaphrus*, 307  
*hesperius* Casey, *Elaphrus*, 303  
*hypocrita* Semenov, *Elaphrus*, 285, 293, 315  
*hypoleucos* (Linnaeus), *Actitis*, 340  
*impressifrons* Chaudoir, *Elaphrus*, 255, 257  
*intermedius* Kirby, *Elaphrus*, 307  
*intermedius* LeConte, *Elaphrus*, 295  
*irregularis* Scudder, *Elaphrus*, 321, 322  
*italicus* Dalla-Torre, *Elaphrus*, 255, 257  
*italicus* Dalla-Torre, *Elaphrus uliginosus*, 255  
*jakovlewi* Semenov, *Elaphrus*, 336, 337  
*japonicus* Uéno, *Elaphrus*, 248, 254, 268, 271, 448, 462, 464  
*julii* LeConte, Blethisa, 226, 238  
*labradorensis* Smetana, Quedius, 245  
*laevigatus* LeConte, *Elaphrus*, 250, 251, 252, 253, 270, 276, 279, 280, 375, 448, 457, 460, 463, 464  
*laevisculptus* Bänninger, *Elaphrus uliginosus*, 255, 257  
*laevisculptus* Reitter, *Elaphrus cupreus*, 255  
*lapponicus* Gyllenhal, *Elaphrus*, 226, 229, 239, 241, 242, 244, 246, 255, 375, 457, 458, 462  
*lapponicus* Gyllenhal, *Elaphrus lapponicus*, 242, 244  
*latipennis* J. Sahlberg, *Elaphrus*, 316, 318  
*latithorax* Schönherr, *Elaphrus*, 257  
*latiusculus* Motschulsky, *Elaphrus*, 314, 315, 460  
*lecontei* Crotch, *Elaphrus*, 285, 286, 287, 288, 289, 291, 293, 294, 295, 298, 303, 304, 306, 308, 309, 311, 319, 375, 451, 463, 464  
*lheritieri* Antoine, *Elaphrus*, 284, 290, 464  
*lindrothi* n. sp., *Elaphrus*, 249, 250, 251, 252, 260, 264, 375, 376, 448, 457, 464  
*littoralis* Dejean, *Elaphrus*, 328, 330  
*longicollis* Sahlberg, *Elaphrus*, 336, 337  
*longicollis* Sahlberg, *Elaphrus angusticollis*, 324, 330, 334, 464  
*lynni* Pierce, *Elaphrus clairvillei*, 271  
*marginicollis* n. sp., *Elaphrus*, 226, 283,

- 284, 288, 306, 311, 375  
*mimus* n. sp., *Elaphrus*, 226, 285, 290, 293, 306, 451  
*multipunctata* (Linnaeus), *Blethisa*, 226, 238  
*multipunctatus* Linnaeus, *Carabus*, 236  
*nevadensis* Jeanne, *Elaphrus pyrenaicus*, 258, 259  
*nigrescens* Letzner, *Elaphrus riparius*, 313  
*normalis* Poppius, *Elaphrus latipennis*, 316  
*obliteratus* Mannerheim, *Elaphrus lapponicus*, 242, 244, 462  
*obscurior* Kirby, *Elaphrus*, 242  
*olivaceus* LeConte, *Elaphrus*, 250, 251, 252, 253, 262, 264, 270, 276, 281, 375, 448, 457, 463  
*orientalis* Semenov, *Elaphrus latipennis*, 316  
*orientalis* Semenov, *Elaphrus tuberculatus*, 316  
*pallipes* Duftschmid, *Asaphidion*, 331  
*pallipes* Duftschmid, *Elaphrus*, 330  
*pallipes* Horn, *Elaphrus*, 330  
*paludosus* Olivier, *Elaphrus*, 315  
*parasimilis* Ball, *Pterostichus*, 245  
*parviceps* Van Dyke, *Elaphrus*, 226, 286, 303, 314, 316, 319, 321, 375, 376, 451, 457, 458, 463, 464  
*pinguedineus* Eschscholtz, *Pterostichus*, 245  
*polita* Faldermann, *Diacheila*, 226, 236, 456, 457, 459  
*politus* Casey, *Elaphrus*, 280  
*politus* LeConte, *Elaphrus*, 271  
*potanini* Semenov, *Elaphrus*, 248, 259  
*punctatissimus* LeConte, *Elaphrus*, 307  
*punctatus* Motschulsky, *Elaphrus*, 233, 258, 322, 323, 326, 327, 457, 463  
*punctatus* Motschulsky, *Elaphrus uliginosus*, 258  
*purkynei* Obenberger, *Elaphrus uliginosus*, 255, 257  
*purpurans* Hausen, *Elaphrus*, 323, 324, 325, 326, 331, 333, 334, 336, 375, 463, 464  
*pyrenoeus* Motschulsky, *Elaphrus*, 248, 258, 276, 375, 376, 448, 460, 462  
*quadricollis* Haldeman, *Blethisa*, 226, 238  
*rhodeanus* Casey, *Elaphrus*, 262, 264  
*riparia* Linnaeus, *Cicindela*, 221, 238, 283, 313  
*riparius* (Linnaeus), *Elaphrus*, 221, 226, 282, 286, 287, 288, 312, 313, 315, 316, 317, 318, 320, 321, 375, 451, 464  
*riparius* Dejean, *Pterostichus*, 245  
*riparius* Nakane, *Elaphrus*, 311  
*riparius* Olivier, *Elaphrus*, 255, 268, 463  
*rubescens* Antoine, *Elaphrus riparius*, 314  
*rubrothoracicus* Goeze, *Paederus*, 340  
*ruficollis* Fabricius, *Paederus*, 340  
*ruscarius foveatus* Pierce, *Elaphrus*, 303, 306  
*ruscarius* Say, *Elaphrus*, 285, 287, 288, 293, 299, 303, 309, 375, 464  
*sibiricus* Motschulsky, *Elaphrus*, 249, 254, 266, 268, 271, 448, 462  
*sibiricus* Uéno, *Elaphrus*, 254  
*similis* LeConte, *Elaphrus*, 299  
*sinuatus* LeConte, *Elaphrus*, 307  
*smaragdiceps* Semenov, *Elaphrus*, 321  
*smaragdinus* Knorlein, *Elaphrus*, 338  
*smaragdinus* Reitter, *Elaphrus*, 328, 330  
*smaragdinus* Reitter, *Elaphrus aureus*, 328  
*smaragdinus* Reitter, *Elaphrus riparius*, 314  
*spissicornis* Casey, *Elaphrus*, 295, 298  
*splendidulus* Motschulsky, *Elaphrus*, 254  
*splendidus* Fisher von Waldheim, *Elaphrus*, 247, 254, 255, 268, 271, 462  
*sylvanus* Goulet, *Elaphrus americanus*, 308, 375, 464  
*tchitcherini* Semenov, *Elaphrus*, 328  
*texanus* Casey, *Elaphrus*, 294  
*tibetanus* Semenov, *Elaphrus*, 286, 314, 316, 320, 451  
*torreyensis* Tanner, *Elaphrus*, 271  
*trossulus* Semenov, *Elaphrus*, 314, 315  
*tschitscherini* Semenov, *Elaphrus*, 328, 329, 330

- tuberculatus* Mäklin, *Elaphrus*, 286, 287,  
288, 309, 314, 315, 316, 318, 319, 320,  
321, 375, 376, 451, 458, 463, 464
- tuberculatus* Mäklin, *Elaphrus riparius*,  
316
- tumidiceps* Munster, *Elaphrus*, 316, 318
- uliginosus* Fabricius, *Elaphrus*, 246, 248,  
254, 255, 257, 259, 260, 375, 376, 448,  
460, 462
- ullrichi* Semenov, *Elaphrus*, 321, 338,  
340, 375
- ulrichi* Redtenbacher, *Elaphrus*, 226, 324,  
325, 326, 338, 340, 445, 451, 463
- ulrichii* Gaubil, *Elaphrus*, 334, 338
- violaceomaculatus* Motschulsky,  
*Elaphrus*, 313, 315, 318, 320
- violaceomaculatus* Motschulsky,  
*Elaphrus riparius*, 314
- viridicupreus* Louvet, *Elaphrus*, 255, 257
- viridis* Horn, *Elaphrus*, 226, 283, 284, 291,  
306, 375, 376, 451
- viridis* Letzner, *Elaphrus riparius*, 291,  
313





## BOOK REVIEWS

CHVALA, M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families Hybotidae, Atelestidae and Microphoridae. Fauna Entomologica Scandinavica, Volume 12. 279 pages containing 639 figures. Scandinavian Science Press Ltd., Langåsen 4, Ganløse, DK - 2760 Måløv, Denmark. Ordinary price 200 D. kr. (discount prices: 140 D. kr. to subscribers for the whole series, and 180 D. kr. to subscribers for Diptera-volumes).

This work presents a long overdue breakdown of the paraphyletic "Empididae" of recent authors into its component taxa, as well as treatments of Scandinavian genera and species now referred to the new or revised family concepts Hybotidae, Atelestidae and Microphoridae. The treatment of the Hybotidae excludes the subfamily Tachydromiinae, which the author already revised in 1975 in Volume 3 of this series. His revision of the Scandinavian true Empididae, which he restricts to the subfamilies Oreogetoninae, Empidinae, Brachystomatinae, Hemerodromiinae and Clinocerinae, is stated to be in preparation and planned to appear in three future volumes. Chvála's concept of Empidoidea agrees with the concept of Orthogenya Brauer (1883), including also the family Dolichopodidae in addition to the families just stated. I prefer the use of Brauer's name, since the ranking of this group as a superfamily (as implied by the -oidea suffix) entails incongruence with the ranking of the subgroups of Cyclorrhapha.

Most of the 52 species described in this work belong to the Hybotidae. Two new species are included, *Oedalea ringdahli* and *O. freyi*. Only 3 and 4 species (respectively) of the relict Atelestidae and Microphoridae are reported for Scandinavia. All described Mesozoic fossils are reviewed and integrated into the phylogenetic analysis. Chvála's descriptions are detailed and well illustrated. His work will no doubt meet with the approval of all specialists working on Orthogenya. But this work is not only of interest to specialists. Chvála has included 60 pages of morphological and systematic discussion, in which he presents much new data contributing to our understanding of the morphological evolution and family-level systematics of the Orthogenya (Empidoidea) and Cyclorrhapha. Of particular interest to me are his conclusions regarding the homologies of the male terminalia, a controversial subject which has generated some extraordinarily misleading literature over the past decade. All students who have been indoctrinated with the still prevalent theory that the clasping organs of male Orthogenya and Cyclorrhapha differ from those of all other insects in being of tergal origin will be well advised to study Chvála's general discussion. In my opinion this theory can no longer be seriously maintained.

Particularly important for understanding the evolution of the male terminalia is Chvála's finding that a reduced true epandrium (9th tergite) is retained in the Empididae in his new restricted sense. He interprets the structure of *Hormopeza* (Figs. 87-89) as indicative of the groundplan condition in this respect, a view with which I concur. Thus I was not correct in stating in my 1972 book that the epandrium was "either lost or fused with cerci" in the groundplan of the Eremoneura (the group inclusive of Orthogenya and Cyclorrhapha). However, this correction need not give comfort to those who maintain that the clasping organs are of tergal origin (as assumed, for instance, in the 1981 Manual of Nearctic Diptera), since *Hormopeza* illustrates exactly the intermediate condition needed to verify my interpretation of the structure of the Cyclorrhapha and of other families of Orthogenya (reduction of the epandrium and dorsal expansion of the gonocoxites, a condition precursory to the elimination of the epandrium and fusion of the gonocoxites across the dorsum which I postulated). The

biarticled gonopods in *Hormopeza* are obviously homologous with those of other Diptera, and Chvála's data indicate that there is no basis in comparative morphology for assuming the replacement of these clasping organs with others of tergal origin. And if the replacement (tergal origin) hypothesis is demonstrably wrong for *Orthogenya*, then it is highly unparsimonious to assume it for the closely related *Cyclorrhapha*.

For the purposes of comprehensive comparative morphology Chvála's treatment of the male genitalia may be criticized for certain omissions. He does not discuss the homology of the paired "hypandrial" apodemes and the bridge joining them, nor does he clarify the origin of what I have called the intergonopodal (formerly interparameral) sclerites, nor does he discuss the groundplan condition and modifications of the gonites (paraphyses). The interpretation of all these structures has been disputed, and certain relevant arguments published by Hennig in 1976 need to be addressed. These omissions are no doubt due to a need for brevity within the present format, rather than to lack of interpretations. I hope that Chvála will be able to supplement his present account with a more detailed morphological paper.

Clarification of the structure of the tip of the female abdomen is also needed. Chvála's interpretation that the tergite and sternite of the 9th segment are well developed in some female *Orthogenya* seems to me difficult to reconcile with the interpretation of female *Cyclorrhapha*. In *Cyclorrhapha* we know (through ontogenetic evidence and the structure of intersexes) that the sclerites of the 9th segment are lacking in females, but the sclerites of the proctiger (10th tergite, 10th sternite and paired cerci) are normally retained. Since the structure of the abdominal tip in females of primitive Empididae, such as *Hormopeza*, resembles that in *Cyclorrhapha*, I think it probable that the sclerites of the 9th segment were already lost in the groundplan of female *Eremoneura* and that all sclerites interpreted by Chvála as belonging to the 9th segment in females really belong to the 10th segment. The phylogenetic conclusions drawn by Chvála (for instance, regarding the invalidity of the view that the presence of acanthophorites groups the Empidoidea within the Asilomorpha) would not be affected by such a change of interpretation.

I have to decide how to break down the *Orthogenya* (Empidoidea) for the Flies of the Nearctic Region, since contributions on parts of this group are presently under discussion. I am in general satisfied with the validity of Chvála's family concepts, and will follow them with one modification. It is clear that his concept of Microphoridae is paraphyletic, since one of its subordinate taxa (Parathalassiini) is demonstrated to be more closely related to the Dolichopodidae. In a strictly cladistic arrangement of monophyletic groups this situation can be handled either by raising the Parathalassiini to family rank or by including them in an expanded concept of Dolichopodidae. In either case the Microphoridae should be restricted to the group called Microphorini by Chvála. The question whether the group *Orthogenya* (Empidoidea) is monophyletic also requires consideration. Chvála regards the Atelestidae as a "monophyletic group of flies very probably sharing a common ancestor with the *Cyclorrhapha*" (p. 70) in agreement with a suggestion in my 1972 book. If this view is correct, then the *Orthogenya* are not monophyletic and several new groupings at a high taxonomic level (the phalanx group of my 1972 book) will need to be named, as will be clear from Chvála's phylogeny diagram (Fig. 140). However, there is some ambiguity in the evidence. For instance, Chandler (1980. *Acta Zool. Acad. Sci. Hung.* 27: 110) has stated that there is only a single spermatheca in the female of *Atelestus*, an apparent synapomorphy with the true Empididae and other families of *Orthogenya* not with the *Cyclorrhapha* (which retain the primitive complement of three spermathecae in their groundplan). The attachment of the paired

apodemes of the male genital segment to the hypandrium is another possible synapomorphy of the Atelestidae with other *Orthogenya* lacking in the Cyclorrhapha (in which these apodemes are fused, forming the unpaired "aedeagal apodeme"). Until further studies have resolved such apparent conflicts of evidence, it appears prudent to retain the concept of *Orthogenya* (Empidoidea) as the sister-group of Cyclorrhapha, as Chvála does in his formal nomenclature.

In conclusion, I wish to congratulate Dr. Chvála for having made such excellent progress with his studies of the *Orthogenya*. His morphological and systematic treatment provides a sound basis for further studies of this hitherto neglected group. His future contributions to this field are awaited with interest. Particularly important will be his treatment of the primitive true empidids included in the Oreogetoninae. North American students of *Orthogenya* and Cyclorrhapha are all strongly advised to read Chvála's general discussion, as it refutes certain interpretations contained in the 1981 Manual of Nearctic Diptera.

Graham C.D. Griffiths  
Department of Entomology  
The University of Alberta  
Edmonton, Alberta T6G 2E3

DUVAL, C. T. (Series Editor). Fauna of New Zealand. Science and Industrial Research, Wellington, New Zealand. MOUND, L. A. and A. K. Walker. 1982. Number 1, Terebrantia (Insecta: Thysanoptera). 113 pp. (\$6.80 U.S.). MC COLL, H. P. 1982. Number 2, Osoriinae (Insecta: Coleoptera: Staphylinidae). 89 pp. (\$6.80 U.S.). HOLLOWAY, B. A. 1982. Number 3, Anthribidae (Insecta: Coleoptera). 264 pp. (\$8.00 U.S.).

Copies are available from: The Publications Office, Science Information Division, DSIR, P. O. Box 9741, Wellington, New Zealand. Cost of overseas mailing is \$1.20 U.S. Standing orders are accepted.

This series about the non-marine invertebrates of New Zealand was inaugurated with appearance of the first three numbers, each of which treats a different group of insects. J. F. Longworth, Director, Entomology Division, DSIR, states in the Preface to the Series (Number 1, pp. 3-4) that the objective is "to provide authoritative and comprehensive guides to identification, in a medium accessible to all would-be users and that will evolve as an accumulating descriptive index of our insects, spiders, mites, and other terrestrial invertebrates". The publisher intends to produce annually about 600 pages in six average-sized contributions.

Because these numbers at hand are the first of what is likely to be a long and important series, it seems appropriate to describe their common properties, for such serve to characterize the series as a whole. Much useful information is found on the attractive tri-colored covers of stiff paper. The front cover has a drawing of a typical adult of one of the included taxa toward the lower left, and a generalized figure representing the form of the main islands of New Zealand toward the upper right. The title of the series is in the upper left, and Number of the particular issue, its title, and names of authors are toward the lower right. On the inside of the front cover, printed in brown, is a generalized map of the "New Zealand Subregion". The outside of the back cover provides general information about the faunal series, including a list of numbers in print, those in press, and those in preparation. Also provided in a single column on the left side are five headings, from top to bottom as follows: "Checklist of Taxa"; "Introduction"; "Key to Taxa"; "Descriptions"; and "Illustrations". On the first page of each of these sections in the text is a broad black line that extends the length of the left margin except for one break in white, which is opposite the appropriate heading on the back cover. Thus, with a quick glance at these easily located pages, one can readily locate the desired section of the volume without having to thumb through the text.

On the inside of the back cover is an outline map illustrating the North and South Island, and Stewart Island. Indicated on each island are area codes and boundaries of an arbitrary system that was developed for recording locality data. Additionally, latitude and longitude are indicated in intervals of 10 minutes by lines which extend to but not across the land areas. The facing page has the same map but without the geographic areas indicated, and with the degree intervals of longitude and latitude extended across the land areas. This is the base map, portions of which are reproduced in the text, in association with information about geographical distribution of each of the species.

Printing is by offset lithography of camera ready copy on high grade glossy paper. The type style is easily read, with headings and captions in easily identified bold-face.

The title pages contain standard information about bibliography and printing, and the name of the insect taxon represented by an illustration on the front cover. Among the names of persons listed are those of the Editorial Advisory Group, and I noted with interest that this committee includes representatives from a university and from the National Museum of New

Zealand, as well as from DSIR. This seems to illustrate the broad level of institutional support accorded to this series.

The text begins with an abstract, followed by a checklist of names of the included taxa. This checklist serves as a detailed table of contents, for the appropriate page number is associated with the name of each taxon. Next is a table of contents followed by acknowledgements. The introductory material preceding keys and descriptions includes information of interest to naturalists generally (notes about phylogeny, ecological generalities about the taxon including host-plant relationships, biogeographic relationships of the New Zealand elements, number of species, *et cetera*), as well as notes about structures that are particularly important in identification of the included taxa. Careful study of this portion of the volume provides a reader with a variety of valuable insights and the information required to use the book for making identifications.

Keys and illustrations are important aids in making identifications, and they are feature components of this series. Illustrations, plentiful and excellent, appear in the form of line drawings emphasizing outlines, as detailed habitus drawings, and as photographs taken with the stereo-electron microscope. Beneath each figure is its number and name (or specific epithet) of the taxon of which it is characteristic. Each issue contains one or more illustrations with structures labelled for ease of recognition, thus facilitating learning those details required to use keys and descriptions.

With the featuring of maps on the covers, one might anticipate that geographical distribution of taxa would be an important component of the species treatments. Indeed it is, for each species of osoriine staphylinid and anthribid of New Zealand (Numbers 2 and 3) an appropriate portion of the standard range map is provided, with positions of localities of collections indicated by dots. Since similar maps are not provided for the terebrant thrips (Number 1) one can infer that the excellent idea to include such diagrams developed after the first part had been completed.

The descriptive section of each number contains the treatments of taxa. These are standard descriptions, with less information provided about structural details for previously described species than for those first described in these volumes. Descriptions of each genus and species in Numbers 2 and 3 include a statement about derivation of the generic name and specific epithet. Number 1 does not include such statements, and I infer that the decision to have such information was made after the terebrant volume was complete. This change and the one involving inclusion of maps for each species illustrate the flexibility of the Editorial Advisory Group and the Series Editor in their attempt to publish a series of the highest quality and of maximum value to naturalists.

Following the descriptive section is the reference section that contains complete citations (with names of serials spelled out) for the abbreviated citations presented in the text.

I have one objection about content, and that concerns the brevity of treatment of evolutionary aspects of the taxa. Inclusion of descriptions of new taxa means that these numbers are not simply handbooks for identification. Rather, they are taxonomic revisions. As such, one might have expected more comprehensive statements than were provided about phylogeny of species and genera, and about origin and development of their distribution patterns in the New Zealand Subregion. Dr. Holloway illustrated the wonderfully evocative transformation series seen in the female genitalia of New Zealand anthribids, and used this as the basis for a linear arrangement of genera in checklist and text. However, she did not extend her notions about evolution of anthribids to the species level. Dr. McColl illustrated the

taxonomic value of the copulatory piece of the genitalia of male osoriines, but then used this complex organ for nothing other than species diagnoses. At least the distribution patterns of the brachypterous species of *Paratrochus* McColl should have been interpreted in terms of vicariance theory as related to Pleistocene refugia of the North and South Islands.

Each number has certain unique features worth noting. Drs. Mound and Walker included brief sections about pest species and natural enemies of terebrant thysanopterans. The volume on osoriines includes a key to the subfamilies of Staphylinidae occurring in the New Zealand Subregion and notes on their status, prepared jointly by Drs. McColl and J. C. Watt. This volume also has SEM photographs illustrating the copulatory pieces of males of all New Zealand osoriine species. Dr. Holloway's volume has habitus drawings of 28 representative anthribids. These illustrations were exquisitely executed by D. W. Helmore, and are worth more than the price of the volume that contains them. Helmore also prepared the habitus illustrations that grace the covers of each of the first three numbers.

A nice touch in Dr. Holloway's volume is a dedication of this number to her former mentor, the distinguished palaeoentomologist Dr. F. M. Carpenter, Museum of Comparative Zoology, Harvard University, on the occasion of his 80th birthday. Inclusion of such a statement, unusual for a series such as this, shows a commendably flexible attitude on the part of the Editor. Most editors of serial publications prefer to live by virtually iron-clad rules of consistency that have a marked potential for generating stereotyped, dull presentation because they prohibit any sparks of expression or imagination that may illuminate a particular issue but that thereby depart from the standard format.

At the asking price, these volumes are virtually a gift to the entomological community. Even non-bibliophiles will be tempted to acquire the entire series. Entomological bibliophiles will be proud to have these volumes on their shelves, for each is truly a showpiece. Specialists in particular taxa will want to have the volumes that concern their special interests, for they will find therein a wealth of valuable information, whether or not they are specifically interested in the fauna of New Zealand. New Zealand invertebrate zoology and invertebrate zoologists will be very well served by this series. Indeed, New Zealand as a nation has been well served by those who conceived and established this series. I look forward with anticipation to its continued development.

G. E. Ball  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3

GRIFFITHS, G. C. D. (Editor). Flies of the Nearctic Region E. Sweitzerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller) Stuttgart, 1982.

The inaugural issues of this series were previously reviewed in *Quaestiones Entomologicae* (Ball, 1980, 16 (3-4): 676-678). Since then, two more numbers have come to my attention, and are briefly reviewed below.

Volume V, Homeodactyla and Asilomorpha, Part 13, Number 3. Bombyliidae, by J. C. HALL and N. L. EVENHUIS, pp. 185-280. (\$36.96, U.S.).

This number begins part way through the description of one species, and ends part way through the description of another. Genera whose species are treated are: *Triploechnus* Edwards (in part); *Lordotus* Loew; *Geminaria* Coquillett; *Sparnopolius* Loew; *Aldrichia* Coquillett; and *Conophorus* Meigen (in part). This is a standard, well illustrated treatment of the species of the groups listed above, and, as noted in my review of the previous part (*Quaest. Ent.* 16: 677) this part is also "uninspiring, of interest mainly to specialists and those who want to name their collections of bee flies". I draw attention to the well executed illustrations of habitus of selected bombyliids representing the genera *Lordotus*, *Geminaria*, *Sparnopolius*, and *Aldrichia*.

I find it unfortunate that an issue should begin and end part way through species accounts. This is no doubt some kind of economy measure, though one could imagine more sinister motives for such a practice.

Volume VIII. Cyclorrhapha II (Schizophora: Calyptratae). Part 2, Number 1. Anthomyiidae, by G. C. D. GRIFFITHS, pp. 1-160. (\$56.32 U.S.).

This number contains a brief general introduction to the Anthomyiidae, a more detailed introduction to the genus *Pegomya* Robineau-Desvoidy, and a thorough taxonomic treatment of most of the species of subgenus *Pegomya*. Although it would seem appropriate to begin treatment of a family with a rather detailed general synopsis, Dr. Griffiths was forestalled in doing so by a generic revision of anthomyiids that will probably be published soon by Dr. V. Michelsen. Nonetheless, potential purchasers might have been offered a little more information than a statement about the unreliability of Hockett's work, and a paragraph about plesiomorphous and apomorphous character states of adult anthomyiids.

The seemingly endless debate among taxonomists about the species problem has been supplanted among dipterists by a seemingly endless debate about homologies of the male genitalia and associated sclerites. Dr. Griffiths devotes about three pages of text to attempt once more to convince his opponents about the correctness of his views. Some of the homologies that he previously proposed have been proven incorrect, but his basic point seems well taken that the genitalia of male cyclorrhaphans have rotated through 360° in the course of ontogeny and phylogeny, and this must be taken into account in comparing structures between such flies and those whose genitalia have rotated less. His assertion is probably correct that the principal cause of opposition by various dipterists is unwillingness to change former interpretations because of the consequentially required changes to an established system of naming these sclerites. He ends this discussion with suggestions for further work to improve understanding of homologies of the genitalic sclerites and those of the postabdomen.

Treatment of the taxa of anthomyiids is phylogenetic. Dr. Griffiths establishes the monophyly of the genus *Pegomya*, and discusses its relationships based on features of adults and larvae. A discursive characterization of the genus is followed by a detailed consideration of the two subgenera *Pegomya* (*sensu stricto*) and *Phoraea* Robineau-Desvoidy, as well as of their sections, subsections, superspecies, and some isolated species not assigned to superspecies. Details of distribution of character states among these taxa are provided in two figures, one for

each subgenus. Unfortunately, the characters are arranged in morphological sequence according to organ system rather than in a sequence by which the reconstructed phylogeny could be visualized. The author also neglects to offer reasons for his classification of character states as plesiomorphous or apomorphous.

In the following text, species of *Pegomya* are arranged hierarchically, with the supraspecific taxa in the same sequence as appears in Fig. 5. (*loc. cit.*, p. 14). The discussion of each supraspecific taxon includes discussion of character states from a phylogenetic point of view, as well as information about host plants of included species.

Treatment of species and subspecies contains the usual taxonomic information. Descriptions of structural features are extensive. Data about host plants and life history are provided for most species. Phylogenetic relationships or chorological affinities receive scant notice.

Geographic ranges are described in terms of states and provinces, with only one map (*loc. cit.*, Fig. 154, p. 126) being used to show the ranges of several species in relation to southern deserts and western salt marshes.

Good line drawings of post abdominal and genitalic sclerites, prepared by the author's wife, Deirdre, admirably supplement the descriptions.

Anthomyiid species are difficult to identify, and probably to classify. It seems that many species are Holarctic, and this adds another dimension to the difficulties of working with the Nearctic members, for one must take into account the Palaearctic fauna. Dr. Griffiths seems to have done excellent, careful work, and he has presented it by means of his characteristic style of clear expository writing. His many references to host plants and way of life show that he thinks about these organisms as living entities, and this adds appreciable interest to the text. Specialists on anthomyiids will no doubt find this issue an excellent one.

It is unlikely, however, that even dipterists interested primarily in other families will find much in this issue to attract their attention. The lack of a general discussion of the family, absence of a key to the species of *Pegomya*, lack of habitus illustrations, virtual lack of distribution maps, and neglect to justify decisions for classification of character states as plesiomorphous or apomorphous rob this issue of more general appeal. This issue even lacks the virtue of being a complete treatment of a single subgenus. The complaint about incomplete individual issues has already been leveled above.

Because of these perceived shortcomings and because of relatively high costs for individual issues in this series, the Editor and publishers of *Flies of the Nearctic Region* might be well advised to reconsider their publication strategy, if they expect to do well in marketing their important and otherwise excellent product.

G. E. Ball  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3



HALFFTER, G. and W. D. EDMONDS. 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae)-- an Ecological and Evolutive Approach. Instituto de Ecologia, México, D. F., 177 pp. (\$40.00 U.S., incl. cost of postage for surface mail; airmail, \$45.00). Order through: Sra. P. Reidl M., Instituto de Ecologia, Apartado Postal 18-845, Delegacion Miguel Hidalgo, 11800, México, D.F.

Beetles of the subfamily Scarabaeinae are about as familiar to non-entomologists of Western European origin as are honey bees, mosquitoes, and dragon flies. Such scarabs were regarded as sacred during various ancient Egyptian dynasties, and such knowledge became a common feature of writings about Egypt by western historians and others. The beetles were and still are a popular motif for those who fashion jewelry. Adult scarabs, rolling their balls of cattle dung, are a common sight in open habitats in the warmer parts of the earth, so much so that they have an English common name ("Tumblebugs"). Scarabaeines have been introduced to the pastures of Australia to assist in removing the cattle dung that has proven to be unacceptable to the indigenous dung beetles of that continent. Thus, at least the habits of the imported scarabaeines are now well known to Australian ranchers.

During the past century, such beetles captured the interest of Jean Henri Fabre; his studies of the way of life of some species and his publications eventually inspired others to undertake further, more extensive studies. Two such individuals are the authors of the volume in question, each having devoted substantial amounts of time and effort to elucidate the way of life of this group of dung beetles.

The resulting book is hard-bound, and is almost square in outline, being about 10" high by 9.75" wide. This uncharacteristic form for books accommodates very well the large illustrations, many of which were designed in such a way that they fit square rather than rectangular pages. Printing and typestyle are of good quality, and the text is easily read. Editing could have been better, for there are numerous minor typographical errors, most of which do not seriously detract from appreciating the meaning of the sentences in which they occur. One omission is troublesome. On page 55 is an untitled and unnumbered table-like figure that can only be Table 2. The latter is referred to in the text, on page 54.

The text comprises a Preface and seven chapters: one, The Scarabaeinae; two, The Ecological Evolution of Scarabaeinae; three, Pattern of Nesting Behavior in Scarabaeinae- an Overview; four, Evolution of Nesting Behavior and Sexual Cooperation; five, Nest Construction and Architecture in Burrowing Scarabaeinae; six, Other Sexual Relationships in Scarabaeinae; seven, The Ovary and Nesting Behavior. Appendix I, a classification of the subfamily Scarabaeinae, lists in systematic order the names of tribes, subtribes, genera, and subgenera of the group.

To provide up-to-date coverage of the literature, a Postscript was added, comprising three more Appendices: II, Nidification Behavior of Old World Oniticellini, by Y. Cambefort; III, Nesting Strategies of Three Species of Coprophagous Scarabaeinae in the Sahel Region of Niger, by C. and R. Rougon; and IV, Commentaries on Recent Literature. Appendices II and III were based on presentations at a symposium held in 1982, in Paris.

The Appendices are followed by a Bibliography and the volume ends with Subject and Taxonomic Indices. Excellent line drawings and diagrams appear at appropriate places in the text to support and illustrate the written statements and arguments.

Organization of the main body of the text is a bit peculiar because the major conclusions are presented in Chapter 4. Thus, Chapters 5 to 7 are in effect appendices that contain supporting data for the conclusions. This organization may have had an unfortunate effect upon the

presentation, because the sharp focus that one looks for in a concluding chapter is not to be found. I believe that this is the result of having the major conclusions presented toward the middle, rather than at the end, of the book: it must be hard for a writer to think in terms of pointed concluding statements when he knows he is writing Chapter 4 of a book with seven chapters!

This book is rich in well-written sections that describe the astonishing range of structures, and ecological and ethological features of scarabaeine beetles. Much of this information was acquired quite recently: a quick count of the dates of references shows that about two-thirds of those cited were published during the past 17 years, that is, since publication of the seminal paper by Halffter and E. G. Matthews ("The natural history of dung beetles of the subfamily Scarabaeinae", 1966, *Folia Entomologica Mexicana*, 12-14: 1- 312). The following brief statement does not do justice to the contents, but gives only an idea about what is included.

Data in the form of behavioral transformation series (ethoclines) are organized in such a way that they support the hypothesis that K-selection (*i.e.*, the response to the adaptive demand to maintain population size by evolution of methods that increase survivability of progeny rather than by production of increased numbers of progeny, any one of whom has rather slight chance of surviving to reproduce) has been the dominant force of evolution in the Scarabaeinae. The elements of these ethoclines are seven more or less distinctive patterns of nesting behavior of adults, defined in terms of 10 features that range from elementary ecological considerations of position of the nest relative to the surface of the ground and proximity to food source, to highly complex ethological considerations of care of the developing brood by the mother. Each pattern is designated by a Roman numeral.

The system is non-hierarchical, though in fact the authors recognize two basic types depending upon whether the nest is prepared first and then food is transported to it (the "burrowing" type), or whether the food is first obtained, removed from the site of its collection, and then a nesting chamber is prepared (the "ball-rolling" type). Patterns I, II, III, and VII are those of burrowers; Patterns IV, V, and VI are those of the ball-rollers. For the burrowers, Pattern I is basic or ancestral; for the ball-rollers, Pattern IV is basic. Increasing numbers in each series refer to increase in some aspects of complexity of behavior patterns. Each series begins with a pattern characterized by lack of parental care of developing young and with construction of a rather simple nest that is about the same as the feeding burrows of the adults, and extends to patterns characterized by complex care of the young by the mother, with preparation of more elaborate types of nests. The more complex types of nesting behavior are associated with production of fewer larvae, but more of these survive to reach maturity. Probably reduced fecundity is reflected in the marked reduction of the female reproductive system to a single ovariole.

The authors emphasize the importance of pair-bonding, culminating in monogamy among those scarabaeines that exhibit the more derived patterns of nesting behavior. The authors also draw attention to bisexual cooperation as a route to subsocial behavior, which is a characteristic feature of the more highly evolved scarabaeines.

It is unfortunate that the authors did not emphasize that their views about evolution of scarabaeines comprise an hypothesis, and did not consider that the most rapid progress in any area of science is likely to come from an alternating sequence of hypothesis testing and reformulation. If they had thought about this, they might have made some predictions based on their hypothesis, with the intention that these be tested as rigorously as possible. They might also have made suggestions about the most fruitful lines of investigation to follow, to provide

crucial new data.

The ethoclines described and their components ought to be of substantial value to phylogenists who are interested in scarabaeines, for the patterns can serve as useful counterpoints to morphological features in a system of reciprocal illumination. Ethological characters are every bit as useful as are morphological, but this seems to be appreciated by few systematists, and hardly at all by those for whom cladograms rather than reconstructed phylogenies have become the goals of systematic study.

Up to the present, hymenopterists have been the major contributors as entomologists to the field of evolutionary comparative ethology, and this is in part because aculeate wasps offer such a fascinating variety of behavioral repertoires. Halffter and Edmonds show in this book that one can find the same sorts of complex behavioral patterns among scarabaeines, and that these are probably major components of the biological success of the group. So, for those ethologists who are not utterly repelled by the sight and smells of the media with which the beetles work, and who do not mind the occasional flecks of feculae under the finger nails (in many ways preferable to the stings of wasps that must be the concern of hymenopterists), tumblebugs offer fine opportunities for study of complex behavior patterns. Although it is unlikely that coleopterists will ever challenge the preeminence of hymenopterists in comparative ethology, the former group has the possibility of making its presence felt in this field through study of scarabaeines.

This book contains a sufficient quantity of good ideas and fascinating data to warrant its purchase and study by systematists and ethologists. I think it would please and interest J. H. Fabre, whose photograph appears as the frontispiece. It would probably make him feel that the seeds planted by him some 85 years ago had produced a fine crop of data and ideas that lead us closer to understanding this exciting group of insects.

G. E. Ball  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3

## EDITOR'S ACKNOWLEDGEMENTS

Volume 19 of *Quaestiones Entomologicae* has been completed, and it is my pleasure as Editor to express appreciation to those who undertook to carry out the required work. Reviews of manuscripts were provided by those whose names are listed below. The appearance of their names does not imply approval of the papers published, but only that they helped me, as requested:

from the Department of Entomology, University of Alberta-- D. A. Craig, D. C. Currie, G. A. P. Gibson, and J. R. Spence;

from the Department of Zoology, University of Alberta-- D. A. Boag and H. F. Clifford; and

from the Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.-- T. L. Erwin.

Other members of my Department graciously assisted with the publishing process, and I thank them. J.-F. Landry provided French translations of several abstracts. I. E. Bergum assisted with correspondence with authors. J. S. Scott and D. Shpeley read proof, as requested. D. A. Craig served as Editor during several of my absences, and W. G. Evans assisted when neither Dr. Craig nor I was available.

Mrs. S. Subbarao, during her fourth year as Publications Manager, continued with her much appreciated high level of performance in attending to the many tasks required of this position.

It was a pleasure to work with the authors who selected this journal for publication of their studies. I hope they will look at their papers with a sense of pride and accomplishment, and that they will continue to have this feeling in the future.

Finally, I thank that small band of faithful subscribers and other unknown readers whose interest in the papers in *Quaest. Ent.* continue to make worthwhile our efforts in the field of publication.

G. E. Ball

# INDEX TO VOLUME 19

- albertaria* (McDunnough), *Traverella*, 88  
*album* (Say), *Ephoron*, 88  
*altermans* (Walker), *Hydropsyche*, 88  
*ameca* n. sp., *Euperilampus*, 3, 6, 8, 12,  
     18, 21  
*ampelus* (Wlk.), *Mericia*, 14  
 Ancyliidae, 66  
 Anderson, J.R., 46  
 Anderson, N.H., 48  
 Anderson, R.L., 74  
*Ankistrodesmus* sp., 45  
*arcticum* Malloch, *Simulium*, 54, 55, 56,  
     60, 67  
 Arctiidae, 14  
*Asellus communis* Say, 74  
 Ashmead, W.H., 14  
 Askew, R.R., 3  
 Augustin, C.L.,  
     *see* Corbet, P.S., 55  
*aureicornis* n. sp., *Euperilampus*, 3, 6, 7,  
     8, 10, 11, 12, 35  
*ayama* Mosely, *Mayatrichia*, 88  
*Bacillus thuringiensis* Berliner, 43  
 Balba, M.H.,  
     *see* Fredeen, F.J.H., 67, 74, 88  
 Bass, J.A.B.,  
     *see* Ladle, M., 45  
*beharae* (Risbec), *Euperilampus*, 35  
*bilineata* (Say), *Hexagenia*, 55  
*blanda* (O.S.), *Eusisyropa*, 14  
*Blondelia hyphantriae* (Tothill), 14  
 Bouček, Z., 2, 3, 6, 7, 11, 13, 14, 15, 34, 35  
 Brachycentridae, 88  
*Brachycentrus occidentalis* Banks, 88  
*brasiliensis* (Ashmead), *Euperilampus*, 3,  
     8, 12, 13, 17, 18, 19, 20, 21, 22  
*brasiliensis* Ashmead, *Perilampus*, 19  
 Burks, B.D., 6, 11, 13, 14, 15  
*Burksilampus* Bouček, 2, 6  
 Burton, G.J., 46, 48  
 Butler, G.L., 74  
*Caenis tardata* McDunnough, 88  
*campyla* Ross, *Cheumatopsyche*, 55  
 Carlsson, M., 46, 48  
 Cerqueira, N.L., 43  
 Chalcidoidea, 2, 4, 6  
 Chance, M.M., , 45, 46  
     *see also* Craig, D.A., 46  
*Cheumatopsyche campyla* Ross, 55  
 Chironomidae, 89  
 Chironomini, 64, 89  
*Chironomus tentans* Fabricius, 74  
 Chlorophyta, 45  
*Chorococcus* sp., 45  
 Chrysolampinae, 3  
*Chrysolampus thenae* (Walker), 3  
 Chrysophyta, 45  
 Clancy, D.W., 3  
 Coleoptera, 88  
*communis* Say, *Asellus*, 74  
*confusa* (Walker), *Hydropsyche*, 88  
 Corbet, P.S., 55  
*Cosmarium* sp., 45  
 Craig, D.A., , 46  
     *see also* Ross, D.H., 46  
 Crawford, J.C., 13  
 Cummins, K.W.,  
     *see also* Anderson, N.H., 48  
 Cummins, K.W., , 48, 64  
     *see* Merritt, R.W., 64  
*cunea* (Drury), *Hyphantria*, 14  
 Cushing, C.E. ,  
     *see* McCullough, D.A., 48  
 Cyanophyta, 45  
 Cymindine Lebiini, 93-216  
     Index to names of taxa, 213-216  
 Darling, D.C., 6, 7, 14  
 Davies, D.M., 45  
 Deason, T.R.,  
     *see* Butler, G.L., 74  
*decorum* Walker, *Simulium*, 74  
 DeFoe, D.L.,  
     *see* Anderson, R.L., 74  
 Dellome, J., 43  
*diarina* (Ross), *Nectopsyche*, 88  
 Diptera, 59, 89  
 Disney, R.H.L., 46  
 Domenichini, G., 6, 7  
*dorsata* Say, *Pteronarcys*, 74  
 Eady, R.D., 4

- Edwards, W.M., 74  
 Elaphrini, 219-477  
     Index to names of taxa, 474-477  
 Elouard, J.-M., 45  
 Elsen, P., 45  
     *see also* Elouard, J.-M., 45  
 Empididae, 89  
*enigma* n. sp., *Euperilampus*, 3, 8, 12, 18,  
     19, 20, 21  
 Ephemeroptera, 59, 64, 75  
*Ephoron album* (Say), 88  
*eumenidarum* Bouček, *Krombeinius*, 7, 34  
*Euperilampoides* Girault, 6, 38  
*Euperilampoides scutellatus* Girault, 6  
*Euperilampus ameca* n. sp., 3, 6, 8, 12, 18,  
     21  
*Euperilampus aureicornis* n. sp., 3, 6, 7, 8,  
     10, 11, 12, 35  
*Euperilampus beharae* (Risbec), 35  
*Euperilampus brasiliensis* (Ashmead), 3,  
     8, 12, 13, 17, 18, 19, 20, 21, 22  
*Euperilampus enigma* n. sp., 3, 8, 12, 18,  
     19, 20, 21  
*Euperilampus gloriosus* (Walker), 3, 6, 7,  
     12, 15  
*Euperilampus hyalinus* (Say), 13  
*Euperilampus hymenopterae* (Risbec), 35  
*Euperilampus iodes* n. sp., 3, 8, 12, 13, 17,  
     18  
*Euperilampus krombeini* Burks, 3, 6, 7, 9,  
     10, 11, 12, 13, 35  
*Euperilampus luteicrus* n. sp., 3, 7, 12, 18,  
     19, 20, 21  
*Euperilampus magnus* n. sp., 3, 6, 8, 12,  
     16  
*Euperilampus mediterraneus* Bouček, 6,  
     35  
*Euperilampus scutellatus* (Girault), 6, 35  
*Euperilampus sensu stricto*, 6  
*Euperilampus sinensis* Bouček, 35  
*Euperilampus solox* n. sp., 3, 8, 12, 13, 16,  
     17  
*Euperilampus spina* Bouček, 35  
*Euperilampus tanyglossa* n. sp., 3, 6, 7, 8,  
     9, 10, 11, 12, 35, 38  
*Euperilampus triangularis* (Say), 3, 6, 8,  
     9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19,  
     20, 21, 22  
*Euperilampus* Walker, 2, 3, 4, 5, 6, 7, 8,  
     11, 21, 34, 35, 38  
*Eusisyropa blanda* (O.S.), 14  
 Fidalgo, A.P., 16, 19, 20  
 Fox, D.L., 4  
*Fragilaria* sp., 45  
 Fredeen, F.J.H., 48, 54, 55, 56, 57, 58, 60,  
     67, 73, 74, 88, 93, 94, 95  
 Fremling, C.R., 55  
 Frost, S.,  
     *see* Kershaw, W.E., 43  
*fugitivus* (Say), *Hyposoter*, 14  
*fulvinotum* Cerqueira and Mello,  
     *Simulium*, 43, 44, 45, 46, 48  
 Gaugler, R., 43, 46  
 Glass, B.L.,  
     *see* Edwards, W.M., 74  
*gloriosus* (Walker), *Euperilampus*, 3, 6,  
     7, 12, 15  
*gloriosus* Walker, *Perilampus*, 6, 15  
 Gorayeb, I.S., 43, 46  
 Graham, M.W.Rdev., 2, 3, 4  
 Harris, R.A., 4  
 Hebrard, G., 45  
 Helson, B.V., 43  
 Hennig, W., 34  
*Hexagenia bilineata* (Say), 55  
*Hexagenia limbata* (Serville), 55  
 Holland, W.J., 19  
*hyalinus* (Say), *Euperilampus*, 13  
*hyalinus* (Say), *Perilampus*, 4, 14  
*Hydropsyche altermans* (Walker), 88  
*Hydropsyche confusa* (Walker), 88  
*Hydropsyche morosa* Hagen, 74  
 Hydroptilidae, 88  
*hymenopterae* (Risbec), *Euperilampus*, 35  
*Hyphantria cunea* (Drury), 14  
*hyphantriae* (Tothill), *Blondelia*, 14  
*Hyposoter* Foerster, 14, 15  
*Hyposoter fugitivus* (Say), 14  
 Ichneumonidae, 14  
*integra* Hald., *Physa*, 74  
*iodes* n. sp., *Euperilampus*, 3, 8, 12, 13,  
     17, 18

- Isonychia sicca* (Walsh), 88  
*Isopterla* Banks, 88  
 Jenkins, W.R.,  
     *see* Ladle, M., 45  
 Kershaw, W.E., 43  
 Klug, M.J.,  
     *see* Cummins, K.W., 48  
 Kovachev, S., 46  
*krombeini* Burks, *Euperilampus*, 3, 6, 7,  
     9, 10, 11, 12, 13, 35  
*Krombeinius* Bouček, 2, 3, 6, 34, 35, 38  
*Krombeinius eumenidarum* Bouček, 7, 34  
 Kurtak, D.C., 45, 46, 48  
 Lacey, L.A., , 45, 46  
     *see also* Mulla, M.S., 45  
 Ladle, M., 45  
 Leptoceridae, 88  
 Lewis, D.L.,  
     *see* Paris, D.F., 74  
*limbata* (Serville), *Hexagenia*, 55  
 Lockhart, W.L.,  
     *see* Sebastien, R.J., 74  
*luggeri* Nicholson and Mickel, *Simulium*,  
     55, 56, 60, 67, 75, 93, 94, 95  
*luteicrus* n. sp., *Euperilampus*, 3, 7, 12,  
     18, 19, 20, 21  
 Maciolek, J.A., 46, 48  
*magnus* n. sp., *Euperilampus*, 3, 6, 8, 12,  
     16  
 Maitland, P.S., 48  
 Matchett, R.E.,  
     *see* Kershaw, W.E., 43  
*Mayatrichia ayama* Mosely, 88  
 McCullough, D.A., 48  
*mediterraneus* Bouček, *Euperilampus*, 6,  
     35  
 Mello, J.A.N.,  
     *see* Cerqueira, N.L., 43  
*Melosira* spp., 45  
*mephitis* (Cameron), *Paraleptomenes*, 34  
*Mericia ampelus* (Wlk.), 14  
*meridionale* Riley, *Simulium*, 67, 94  
 Merritt, R.W., , 64  
     *see* Wallace, J.B., 45, 46  
*micans* Dalman, *Perilampus*, 34  
 Mills, M.L.,  
     *see* Kershaw, W.E., 43  
 Minshall, G.W.,  
     *see* McCullough, D.A., 48  
*minutus* Traver, *Tricorythodes*, 88  
 Mites, 67, 73, 74, 89, 93  
 Mokry, J.E., 48  
 Molloy, D.,  
     *see* Gaugler, R., 43, 46  
*Monacon* Waterston, 2, 3, 6  
 Moore, J.W., 45, 46  
*morosa* Hagen, *Hydropsyche*, 74  
 Muirhead-Thomson, R.C., 74  
 Mulla, M.S., , 45  
     *see also* Lacey, L.A., 45, 46  
 Munroe, E. G., 55  
*Nectopsyche diarina* (Ross), 88  
*nesiotes* Crawford, *Perilampus*, 34  
*Nesoperilampus* Rohwer, 6  
*Nesoperilampus typicus* Rohwer, 6  
 Nilsson, L.M.,  
     *see* Carlsson, M., 46, 48  
*Nitzschia* sp., 45  
 O'Kelly, J.C.,  
     *see* Butler, G.L., 74  
*occidentalis* Banks, *Brachycentrus*, 88  
 Odonata, 88  
*Oedogonium* sp., 45  
 Orthocladinae, 89  
*Oscillatoria* sp., 45  
*Paraleptomenes mephitis* (Cameron), 34  
 Paris, D.F., 74  
 Parker, H.-L., 3  
 Pavlichenko, V.I., 48  
 Peck, O., 14  
 Perilampidae, 2, 34  
 Perilampinae, 2  
*Perilampus brasiliensis* Ashmead, 19  
*Perilampus gloriosus* Walker, 6, 15  
*Perilampus hyalinus* (Say), 4, 14  
*Perilampus Latreille*, 2, 3, 4, 6, 7, 34, 35,  
     38  
*Perilampus micans* Dalman, 34  
*Perilampus nesiotes* Crawford, 34  
*Perilampus punctiventris* Crawford, 34  
*Perilampus singaporensis* Rohwer, 34  
*Perilampus triangularis* Say, 13  
 Peterson, D.J., 55  
*Physa integra* Hald., 74

- Pinger, R.R.,  
     *see* Gorayeb, I.S., 43  
 Plecoptera, 59, 88  
 Principi, M.M., 3, 48  
 Pteromalidae, 2  
*Pteronarcys dorsata* Say, 74  
*punctiventris* Crawford, *Perilampus*, 34  
 Quillévéré, D.,  
     *see also* Elsen, P., 45  
 Richards, O.W., 4  
 Riek, E. F., 6, 7  
 Ross, D.H., 46  
 Saha, J.G.,  
     *see* Fredeen, F.J.H., 67, 74, 88  
*salicetum* (Steffan), *Steffanolampus*, 7,  
     34  
 Schmid, F.,  
     *see* Corbet, P.S., 55  
 Schröder, P., 45, 46  
*scutellatus* (Girault), *Euperilampus*, 6, 35  
*scutellatus* Girault, *Euperilampoides*, 6  
 Sebastien, R.J., 48, 74  
 Serra-Tosio, B., 46  
 Shehvenko, A.K.,  
     *see* Pavlichenko, V.I., 48  
*sicca* (Walsh), *Isonychia*, 88  
 Simuliidae, 66, 89  
*Simulium arcticum* Malloch, 54, 55, 56,  
     60, 67  
*Simulium decorum* Walker, 74  
*Simulium fulvinotum* Cerqueira and  
     Mello, 43, 44, 45, 46, 48  
*Simulium luggeri* Nicholson and Mickel,  
     55, 56, 60, 67, 75, 93, 94, 95  
*Simulium meridionale* Riley, 67, 94  
*Simulium vittatum* Zetterstedt, 46, 48,  
     67, 73, 93  
*sinensis* Bouček, *Euperilampus*, 35  
*singaporensis* Rohwer, *Perilampus*, 34  
*Sinophorus validus* (Cresson), 14  
 Sioli, H., 43  
 Smith, H.S., 3  
 Smulyan, M.T., 4, 34  
*solox* n. sp., *Euperilampus*, 3, 8, 12, 13,  
     16, 17  
 Sphaeridae, 66  
*spina* Boucek, *Euperilampus*, 35  
*Spirulina* sp., 45  
 Spurr, D.T.,  
     *see* Fredeen, F.J.H., 57, 58  
 Steblyuk, M.V.,  
     *see* Pavlichenko, V.I., 48  
*Steffanolampus* Peck, 2, 4, 6  
*Steffanolampus salicetum* (Steffan), 7, 34  
 Svensson, Bj.,  
     *see* Carlsson, M., 48  
 Syme, P.D.,  
     *see* Davies, D.M., 45  
*Tabellaria* spp., 45  
 Tachinidae, 14  
 Tadic, M.,  
     *see* Warren, L.O., 14  
*tanyglossa* n. sp., *Euperilampus*, 3, 6, 7, 8,  
     9, 10, 11, 12, 35, 38  
 Tanypodini, 89  
 Tanytarsini, 64, 89  
*tardata* McDunnough, *Caenis*, 88  
*tentans* Fabricius, *Chironomus*, 74  
*thenae* (Walker), *Chrysolampus*, 3  
*thuringiensis* Berliner, *Bacillus*, 43  
*Traverella albertaria* (McDunnough), 88  
*triangularis* (Say), *Euperilampus*, 3, 6, 8,  
     9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19,  
     20, 21, 22  
*triangularis* Say, *Perilampus*, 13  
 Trichoptera, 55, 59, 88  
*Tricorythodes minutus* Traver, 88  
 Tunzi, M.G., 46, 48  
*typicus* Rohwer, *Nesoperilampus*, 6  
 Ulfstrand, S.,  
     *see* Carlsson, M., 46, 48  
*validus* (Cresson), *Sinophorus*, 14  
*vittatum* Zetterstedt, *Simulium*, 46, 48,  
     67, 73, 93  
 Walker, F., 6, 15  
 Wallace, J.B., 45, 46  
 Warren, L.O., 14  
 West, A.S.,  
     *see* Helson, B.V., 43  
 Whipple, G.C.,  
     *see* Ward, H.B., 66  
 Whitton, B.A., 48, 66  
 Williams, T.R.,  
     *see* Kershaw, W.E., 43



Wotton, R.S., , 45, 46, 48

*see* Carlsson, M., 46, 48



















Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required: one in English, and one in another language, preferably French.

Tables, including titles and footnotes, must not be more than 7 3/4 X 4 3/4 inches (19.7 X 12.1 cm). Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 3/4 X 5 inches, or 19.7 X 13.2 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

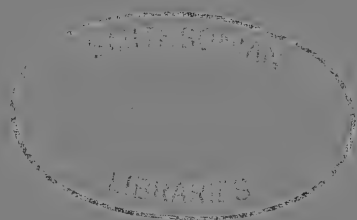
Subscription rates are the same for institutions, libraries and individuals, \$17.00 per volume of four issues, normally appearing at quarterly intervals; single issues \$5.00. Back volumes and issues are available at the same cost. There is a postal surcharge of \$4.00 to subscribers outside Canada. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to:

The Editor, *Quaestiones Entomologicae*  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3

QAL  
461  
515  
514

# Quaestiones Entomologicae



A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada



A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 20

Numbers 1-4

1984

## CONTENTS

Bousquet—Nomenclatural Notes on Nearctic Pterostichini (Coleoptera: Carabidae)	1
Frank and Thomas—Cocoon-Spinning and the Defensive Function of the Median Gland in Larvae of Aleocharinae (Coleoptera, Staphylinidae): A Review	7
Steiner—Observations on the Possible Use of Habitat Cues and Token Stimuli by Caterpillar-Hunting Wasps: <i>Euodyneros foraminatus</i> (Hymenoptera, Eumenidae)	25
Shepard—Type Locality Restrictions and Lectotype Designations for the "Rocky Mountain" Butterflies Described by Edward Doubleday in "The Genera of Diurnal Lepidoptera" 1847-1849	35
Book Review—Andersen, N. Møller, 1982. The Semiaquatic Bugs (Hemiptera: Gerrhomorpha), Phylogeny, Adaptations, Biogeography and Classification	45
Stanger—Preliminary Observations on Genetic Variations in Three Colonies of <i>Musca domestica</i> (Diptera: Muscidae) Isolated from Central Alberta	51
Ratcliffe—A Review of the Penichrolucaninae with Analyses of Phylogeny and Biogeography, and Description of a Second New World Species from the Amazon Basin (Coleoptera: Lucanidae)	60
Gooding—Tsetse Genetics: A Review	89
Ashe—Generic Revision of the Subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with Review of the Described Subgenera and Major Features of Evolution	129
Erwin and Sims—Carabid beetles of the West Indies (Insecta: Coleoptera): A Synopsis of the Genera, and Checklists of Tribes of Caraboidea, and of the West Indian Species	350
Book Review—Kryzhanovsky, O.L. 1983. Fauna of the U.S.S.R., new series no.128. Coleoptera. Volume 1, no. 2	467
Editor's Acknowledgements	469
Index to Volume 20	471



A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 20

Number 1

1984

# CONTENTS

Bousquet–Nomenclatural Notes on Nearctic Pterostichini (Coleoptera: Carabidae) . . . . .	1
Frank and Thomas–Cocoon-Spinning and the Defensive Function of the Median Gland in Larvae of Aleocharinae (Coleoptera, Staphylinidae): A Review . . . . .	7
Steiner–Observations on the Possible Use of Habitat Cues and Token Stimuli by Caterpillar-Hunting Wasps: <i>Euodynerus foraminatus</i> (Hymenoptera, Eumenidae) . . . . .	25
Shepard–Type Locality Restrictions and Lectotype Designations for the “Rocky Mountain” Butterflies Described by Edward Doubleday in “The Genera of Diurnal Lepidoptera” 1847–1849 . . . . .	35
Book Review–Andersen, N. Møller. 1982. The Semiaquatic Bugs (Hemiptera: Gerromorpha). Phylogeny, Adaptations, Biogeography and Classification. . . . .	45





NOMENCLATURAL NOTES ON NEARCTIC PTEROSTICHINI  
(COLEOPTERA: CARABIDAE)

Yves Bousquet  
Biosystematics Research Institute  
Agriculture Canada  
Ottawa K1A 0C6

*Quaestiones Entomologicae*  
20: 1-5 1984

ABSTRACT

*The author points out that the generic name Evarthrus LeConte 1852 must be replaced by Cyclotrachelus Chaudoir 1838. The following new synonyms (with the senior synonym in parenthesis) are proposed: Evarthrus perseverus Motschulsky (=Feronia moesta Say), Evarthrus basilaris Motschulsky (=Evarthrus convivus LeConte), Evarthrus licinoides Motschulsky (=Feronia sodalis LeConte), Evarthrus nimius Motschulsky (=Feronia sigillata Say), Eumolops decepta Casey and Pterostichus texicola Csiki (=Evarthrus texanus Motschulsky = Cyclotrachelus torvus texanus Motschulsky). Four type-species are designated: Feronia imitatrix Tschitschérine (=Feronia haematopus Dejean) for Boreobia Tschitschérine (=Stereocerus Kirby), Feronia castanea Dejean for Hypherpes Chaudoir, Pterostichus tarsalis LeConte for Pheryphes Casey and Feronia nivalis F. Sahlberg for Pseudocryobius Motschulsky (=Cryobius Chaudoir).*

RÉSUMÉ

*L'auteur fait remarquer que le nom générique Evarthrus LeConte 1852 doit être remplacé par Cyclotrachelus Chaudoir 1838. Les synonymes suivants (avec le synonyme ancien entre parenthèses) sont proposés pour la première fois: Evarthrus perseverus Motschulsky (=Feronia moesta Say), Evarthrus basilaris Motschulsky (=Evarthrus convivus LeConte), Evarthrus licinoides Motschulsky (=Feronia sodalis LeConte), Evarthrus nimius Motschulsky (=Feronia sigillata Say), Eumolops decepta Casey et Pterostichus texicola Csiki (=Evarthrus texanus Motschulsky = Cyclotrachelus torvus texanus Motschulsky). L'espèce-type est désignée pour quatre taxa: Feronia imitatrix Tschitschérine (=Feronia haematopus Dejean) pour Boreobia Tschitschérine (=Stereocerus Kirby), Feronia castanea Dejean pour Hypherpes Chaudoir, Pterostichus tarsalis LeConte pour Pheryphes Casey et Feronia nivalis F. Sahlberg pour Pseudocryobius Motschulsky (=Cryobius Chaudoir).*

This paper provides some nomenclatural notes on Nearctic Pterostichini (*sensu stricto*). The proper use of the generic name *Evarthrus* LeConte is discussed, five species described by Motschulsky (1865) are examined and the type-species of four taxa are proposed.

ON THE PROPER USE OF THE NAME *EVARTHURUS* LECONTE

In 1852, LeConte erected the genus *Evarthrus* and pointed out (p. 225):

"The second of these [*Evarthrus* Lec.] was already established by Chaudoir upon a single species under the name *Cyclotrachelus*, which is totally inapplicable to most of the species of the genus as here set forth: as, moreover, Baron Chaudoir would probably refuse to consider my group as constituting a single genus, corresponding with his *Cyclotrachelus*, I have felt myself compelled to adopt a new name, leaving to those who may wish still farther to divide the genus, the power to restoring *Cyclotrachelus* to the particular set of species for which it was intended."

For more than two decades, both *Evarthrus* LeConte and *Cyclotrachelus* Chaudoir were considered as valid subgenera of one genus, but all authors (e.g., Ball 1960, Freitag 1969, Erwin *et al.* 1977, Thompson 1979) have retained the name *Evarthrus* LeConte for the genus. Since Chaudoir's name is older than LeConte's name, *Cyclotrachelus* Chaudoir is the valid name for the genus (I.C.Z.N., Article 23 (e) (i)). The nomenclature of the genus is summarized as follows (subgeneric synonyms are not listed):

Genus *Cyclotrachelus* Chaudoir 1838, type-species: *Feronia tenebricosa* Dejean (= *Molops faber* Germar) (by monotypy).<sup>1</sup>

subg. *Fortax* Motschulsky 1865, type-species: *Feronia morio* Dejean (designated by Freitag 1969: 101).

subg. *Cyclotrachelus* s. str.

subg. *Evarthrus* LeConte 1852, type-species: *Feronia sigillata* Say (designated by Casey 1918: 322).

### NEW SYNONYMIES

In 1865, Motschulsky described five new species of the genus *Evarthrus* LeConte (= *Cyclotrachelus* Chaudoir). These species were overlooked by Freitag (1969) in his taxonomic revision of the genus probably because Csiki (1930), without giving a reason, listed them under the subgenus *Cryobius* Chaudoir of *Pterostichus* Bonelli. Through the courtesy of Dr. N. Nikitsky of Moscow University, USSR, I have had the opportunity to study the type material of these species.

#### *Evarthrus perseverus*

Motschulsky's collection contains a single female specimen under this name (Cf. Keleinikova 1976), with the following labels: "Type"/"Evarthrus perseverus Motch Am.bor.)/red square label. The label "LECTOTYPE, Evarthrus perseverus Motsch., des. 1983, Y. Bousquet" has been attached to it. The specimen agrees with those of *Pterostichus moestus* (Say) and consequently *Evarthrus perseverus* Motschulsky (1865) is a junior synonym of *Feronia moesta* Say (1823) (*syn. nov.*). The lectotype is in poor condition with both antennae (except for the basal segment of the right antenna), palpi (except for the basal segment of the right labial palpus and the left maxillary palpus), both anterior legs (except for the coxa and trochanter), the left median leg (except for the coxa and trochanter), all tarsi of the posterior legs, part of the last abdominal segment and the genitalia missing.

#### *Evarthrus basilaris*

A single male specimen is present under this name in Motschulsky's collection (Cf. Keleinikova 1976). It bears the following labels: small green disc/"Type"/"Evarthrus basilaris Motch. Am.b.Mobile)/red square label. The label "LECTOTYPE, Evarthrus basilaris Motsch., des. 1983, Y. Bousquet" has been attached to it. The specimen agrees with those of *Cyclotrachelus convivus* (LeConte) and consequently *Evarthrus basilaris* Motschulsky (1865)

---

<sup>1</sup>The designation of *Molops faber* Germar by Freitag (1969: 109) and *Cyclotrachelus roticollis* Casey (= *Molops faber* Germar) by Casey (1918: 348) is invalid since these taxa were not originally included by Chaudoir.

is a junior synonym of *Evarthrus convivus* LeConte (1852) (*syn. nov.*). Both antennae (except for the first 2 segments of the right antenna), both maxillae, the last 2 segments of both labial palpi, all tarsal segments (except for the basal segment of the left leg) of both anterior legs, the last tarsal segment and part of the femur of the left median leg, the last 3 tarsal segments and part of the femur of the right median leg, all tarsal segments of the right posterior leg, the femur (except for the extreme basis), tibia and tarsal segments of the left posterior leg and the genitalia are missing in the lectotype.

#### *Evarthrus licinoides*

Motschulsky's collection contains a single female specimen under this name (Cf. Keleinikova 1976), with the following labels: "N.O." (on a small green disc)/"Type"/"Evarthrus licinoides Motch. Am.bor.)/red square label. The label "LECTOTYPE, Evarthrus licinoides Motsch., des. 1983, Y. Bousquet" has been added to it. The specimen agrees with those of *Cyclotrachelus sodalis sodalis* (LeConte) and consequently *Evarthrus licinoides* Motschulsky (1865) is a junior synonym of *Feronia sodalis* LeConte (1848) (*syn. nov.*). The specimen has both antennae (except for the basal segment of the left antenna and the first 3 segments of the right antenna) and maxillary palpi, the last 2 segments of both labial palpi, the last tarsal segment of the right anterior leg, the apical part of the femur, the tibia and the tarsal segments of the right median and posterior legs, all tarsal segments of the left posterior leg, a large section of the abdomen (including the last 3 segments) and the genitalia missing.

#### *Evarthrus nimius*

Motschulsky's collection probably contains only one specimen under this name<sup>2</sup>. The female specimen I have seen bears the following labels: "S.E. Pa se-VIII" / "Pter. sigillata" / "Type" / "Evarthrus nimius Motch. Am.bor."<sup>3</sup>. The label "LECTOTYPE, Evarthrus nimius Motsch., des. 1983, Y. Bousquet" has been attached to it. The specimen agrees with those of *Cyclotrachelus sigillatus* (Say) and consequently *Evarthrus nimius* Motschulsky (1865) is a junior synonym of *Feronia sigillata* Say (1823) (*syn. nov.*). The specimen has the last 9 segments of both antennae, the last segment of each labial palpus, the right maxillary palpus, the last 2 segments of the left maxillary palpus and the genitalia missing.

#### *Evarthrus texanus*

One female specimen is included under this name in Motschulsky's collection (Cf. Keleinikova 1976). It bears the following labels: "Type"/"Evarthrus texanus Motch. Am.bor.)/red square label. The label "LECTOTYPE, Evarthrus texanus Motsch., des. 1983, Y. Bousquet" has been attached to it. The specimen agrees with those of *Cyclotrachelus torvus deceptus* (Casey 1918). As Motschulsky's name is older than Casey's name, the valid name of the taxon is *C. torvus texanus* (Motschulsky 1865) and consequently *Eumolops decepta* Casey (*syn. nov.*), along with *Eumolops impolita* Casey and *Evarthrinus minax* Casey listed by Freitag (1969: 162) as synonyms of *C. torvus deceptus*, are junior synonyms of *Evarthrus texanus* Motschulsky. Furthermore, because *E. texanus* became a junior secondary homonym

---

<sup>2</sup>The species is not listed by Keleinikova (1976).

<sup>3</sup>According to Motschulsky (1865: 260), the specimen is from Ohio.

of *Pterostichus* (*Poecilus*) *texanus* LeConte (1863) when *Evarthrus* (= *Cyclotrachelus*) and *Poecilus* were regarded as subgenera of *Pterostichus*, Csiki (1930: 659) changed Motschulsky's name to *Pterostichus texicola*. However, *Evarthrus* is actually considered as a distinct genus from *Pterostichus*, as *Poecilus* should be (Bousquet, unpublished data), and consequently *Pterostichus texicola* Csiki is here listed as a junior objective synonym of *Evarthrus texanus* Motschulsky (*syn. nov.*). Both antennae (except for the first 3 segments), the last segment of the left maxillary palpus, the last tarsal segment of both anterior legs, both median and the left posterior leg (except for the coxa and trochanter) and the right posterior leg are missing in the lectotype.

## TYPE-SPECIES DESIGNATIONS

Four supraspecific taxa of Pterostichini listed (under *Pterostichus* Bonelli) by Erwin *et al.* (1977) are left without valid type-species designations. For each of these taxa, I designate here a type-species from the species originally included.

*Boreobia* Tschitschérine 1896, type-species: *Feronia imitatrix* Tschitschérine (= *Feronia haematopus* Dejean) (present designation). *Boreobia* is a junior subjective synonym of *Stereocerus* Kirby (1837).

*Hypherpes* Chaudoir 1838, type-species: *Feronia castanea* Dejean (present designation). Originally, Chaudoir (1838:8) designated as the type-species *Platysma amethystinum* but the name remained a manuscript name until 1843 (Mannerheim 1843: 201) and was therefore not available. The designation of *Feronia valida* Dejean (= *Pterostichus algidus* LeConte) as the type-species of *Hypherpes* by Casey (1918: 321) is invalid since the species was not originally included by Chaudoir in the taxon.

*Pheryphes* Casey 1920, type-species: *Pterostichus tarsalis* LeConte (present designation; first species name recorded [1. c., p. 186]).

*Pseudocryobius* Motschulsky 1850, type-species: *Feronia nivalis* F. Sahlberg (present designation; first name recorded in list of included species [1. c., p. 54]). *Pseudocryobius* is a junior subjective synonym of *Cryobius* Chaudoir (1838).

## ACKNOWLEDGEMENTS

I thank Dr. Richard Freitag of Lakehead University, Thunder Bay, for his courtesy during my two day visit at Thunder Bay and for checking the identification of Motschulsky's types. I also wish to thank Dr. N. Nikitsky of Moscow University, Moscow, USSR, for sending me Motschulsky's material.

The assistance of my colleagues Drs. J.M. Campbell, A. Smetana and J.R. Vockeroth for their criticisms of the manuscript is gratefully acknowledged.

## REFERENCES

- Ball, G.E., 1960. Carabidae (Latreille, 1810): pp. 55–181. In Arnett, R.H. Jr. The Beetles of the United States. Washington (D.C.), Catholic University of America Press. 1112 pp.
- Casey, T.L., 1918. Studies among some of the American Amarinae and Pterostichinae. "Memoirs on the Coleoptera", vol. 8: pp. 224–393. Lancaster, PA, The New Era Printing Company.

- Casey, T.L., 1920. Random studies among the American Caraboidea. "Memoirs on the Coleoptera", vol. 9: pp. 133–299. Lancaster, PA, The New Era Printing Company.
- Chaudoir, M. de, 1838. Tableau d'une nouvelle subdivision du genre *Feronia* Dejean suivi d'une caractéristique de trois nouveaux genres de Carabiques. Bulletin de la Société Impériale des Naturalistes de Moscou, 11: 3–32.
- Csiki, E., 1930. Harpalinae IV. In Junk, W. and S. Schenkling (eds.). Coleopterorum catalogus. Vol. II. Carabidae II. Pars 112: 529–738. Berlin.
- Erwin, T.L., Whitehead, D.R. and G.E. Ball, 1977. Family 4. Carabidae, The Ground Beetles. In R.E. Blackwelder and R.H. Arnett Jr. Checklist of the beetles of Canada, United States, Mexico, Central America, and the West Indies (yellow version). Kinderhook, NY. World Digest Publications. 4.1–4.68.
- Freitag, R., 1969. A revision of the species of the genus *Evarthrus* LeConte (Coleoptera: Carabidae). Quaestiones Entomologicae, 5: 88–211.
- Keleïnikova, S.I., 1976. V.I. Motschulsky's types of Coleoptera in the Collection of the Zoological Museum MGU. I. Carabidae (in Russian). Sbornik trudov Gosudarstvennogo zoologicheskogo muzeya, 15: 183–224.
- Kirby, W., 1837. Part IV. Insecta. In J. Richardson. Fauna Boreali-Americana; or the zoology of the Northern Parts of British America: containing descriptions of the objects of Natural History collected on the late northern land expeditions, under command of captain Sir John Franklin, R.N. Norwich. 249 pp.
- LeConte, J.L., 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York, 4: 173–474.
- LeConte, J.L., 1852. Synopsis of the species of *Pterostichus* Bon. and allied genera inhabiting temperate North America. Journal of the Academy of Natural Sciences of Philadelphia, ser. II, 2: 225–256.
- LeConte, J.L., 1863. New species of North American Coleoptera. Smithsonian Miscellaneous Collections, 167: 1–86.
- Mannerheim, C.G., 1843. Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sitkha und Neu-Californiens. Bulletin de la Société Impériale des Naturalistes de Moscou, 16: 175–314.
- Motschulsky, V. von, 1850. Die Kaefer Russlands. I. Insecta Carabica. Moscow, Gautier. 91 pp.
- Motschulsky, V. von, 1865. Énumération des nouvelles espèces de Coléoptères rapportés de ses voyages. Bulletin de la Société Impériale des Naturalistes de Moscou, 38: 227–313.
- Say, T., 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Transactions of the American Philosophical Society, 2: 1–109.
- Thompson, R.G., 1979. A systematic study of larvae in the Tribes Pterostichini, Morionini, and Amarini (Coleoptera: Carabidae). Agricultural Experiment Station, University of Arkansas, Bulletin 837. 105 pp.
- Tschitschérine, T., 1896. Note sur deux nouvelles formes arctiques du genre *Feronia* Latr. Dej. Annuaire du Musée zoologique de l'Académie impériale des sciences de St. Pétersbourg, 1: 373–377.



# COCOON-SPINNING AND THE DEFENSIVE FUNCTION OF THE MEDIAN GLAND IN LARVAE OF ALEOCHARINAE (COLEOPTERA, STAPHYLINIDAE): A REVIEW<sup>1</sup>

J. H. Frank

Florida Medical Entomology Laboratory

200 9th Street S.E.

Vero Beach, Fl 32962

U.S.A.

M. C. Thomas

4327 NW 30th Terrace

Gainesville, Fl 32605

U.S.A.

*Quaestiones Entomologicae*

20: 7-23 1984

## ABSTRACT

*Ability of a Leptusa prepupa to spin a silken cocoon was reported by Albert Fauvel in 1862. A median gland of abdominal segment VIII of a Leptusa larva was described in 1914 by Paul Brass who speculated that it might have a locomotory function, but more probably a defensive function. Knowledge was expanded in 1918 by Nils Alarik Kemner who found the gland in larvae of 12 aleocharine genera and contended it has a defensive function. He also suggested that cocoon-spinning may be a subfamilial characteristic of Aleocharinae and that the Malpighian tubules are the source of silk. Kemner's work has been largely overlooked and later authors attributed other functions to the gland. However, the literature yet contains no proof that Kemner was wrong even though some larvae lack the gland and even though circumstantial evidence points to another (perhaps peritrophic membrane) origin of the silk with clear evidence in some species that the Malpighian tubules are the source of a nitrogenous cement. The degree of development of the gland varies among tribes of Aleocharinae with a higher level of development occurring in what are now considered the most derived tribes. Developmental state of the median gland and the ability to spin a cocoon may help elucidate the phylogeny of Aleocharinae.*

## RÉSUMÉ

*La capacité de la pupa de Leptusa à filer un cocon de soie a été rapportée par Albert Fauvel en 1862. En 1914, Paul Brass décrit une glande médiane sur le huitième segment abdominal de la larve de Leptusa et il supposa qu'elle pouvait avoir une fonction locomotrice ou, plus probablement, une fonction défensive. Les connaissances sur cette glande ont été étendues en 1918 par Nils Alarik Kemner qui la trouva chez les larves de 12 genres d'Aléocharinés et qui soutint qu'elle avait une fonction défensive. Il suggéra également que la filature d'un cocon puisse être une caractéristique de la sous-famille des Aleocharinae et que les tubes de Malpighi soient la source de soie. Le travail de Kemner a été largement ignoré et les auteurs subséquents attribuèrent d'autres fonctions à la glande. Cependant la littérature ne contient aucune preuve indiquant que Kemner était dans l'erreur, bien que certaines larves n'aient pas de glandes, que des preuves indirectes indiquent une origine différente de la soie (peut-être la membrane péritrophique) et que des preuves nettes montrent que chez certaines espèces, les tubes de Malpighi sont la source d'un ciment azoté. Le degré de développement de la glande varie selon les tribus d'Aleocharinae, un niveau de développement plus élevé se rencontrant chez les tribus*

---

<sup>1</sup>University of Florida, Institute of Food and Agricultural Sciences, Journal Series no. 4633

*considérées comme les plus dérivées. L'état de développement de la glande médiane et la capacité à filer un cocon peuvent aider à élucider la phylogénie des Aleocharinae.*

Arnett (1961) wrote that aleocharines were the most poorly known of all beetles. Unfortunately, that situation remains the same two decades later. If knowledge of the adults of this taxonomically difficult group is inadequate, knowledge of the immature stages lags so far behind that larvae collected in the field usually cannot be identified even to tribe. This is true even though many aleocharine larvae have been described; however, many descriptions of larvae identified only by association with adults (*ex societate imaginis*) are of doubtful validity. Since the current classification of the Aleocharinae is based solely on the structure of the adults, increased knowledge of the larvae, through thorough descriptions of reared larvae placed in the context of the existing literature to allow discrimination between tribal, generic and specific characters, should help provide a better understanding of the phylogeny of this huge group.

Because of the small size of aleocharine larvae, only the larger and more obvious structures have been described for many taxa. Among these is the median gland (sometimes called the dorsal gland) of abdominal segment VIII. When it is darkly pigmented and protuberant, the gland is readily visible, and in some larvae it even overhangs tergite IX. Another obvious character is the cocoon-spinning ability of the prepupa of many aleocharine genera.

What is the ecological, phylogenetic, and behavioral significance of cocoon-spinning? Where are the glands that produce the silk and what is their structure? What is the physiological manner of its production? What were the genetic and evolutionary pathways that led to cocoon-spinning? The presence of a median gland raises a similar group of questions. Unfortunately, even though both the median gland and cocoon-spinning have been known in the literature for more than a century, not one of those questions can be answered.

This paper is concerned principally with: 1) reviewing the literature as it pertains to the median gland and cocoon-spinning; 2) compiling the known distribution of these two characters among the tribes of the Aleocharinae; and, 3) assessing the potential of these characters toward elucidating phylogenetic relationships within the subfamily and between the Aleocharinae and the rest of the Staphylinidae. Cocoon-spinning and glands of other staphylinid larvae as well as the tergal gland of aleocharine adults are discussed insofar as they relate to the objectives.

## THE MEDIAN GLAND OF ALEOCHARINE LARVAE

Perris (1853) mentioned and illustrated a protuberant dorsal structure of abdominal segment VIII, extending posteriorly over segment IX in larvae of *Phloeopora*. He did not attribute a function to this structure. Some other aleocharine larvae were found to have similar structures by Fauvel (1862, 1875) and Rey (1887) (Table 1).

Recognizing the glandular nature of the protuberance, Brass (1914) sectioned, described and illustrated a structure consisting of four groups of glands connected to a large reservoir opening at the apex of the protuberance. He placed an unidentified larva (attributed by Kemner (1918) and Verhoeff (1919) to *Leptusa*) between two narrowly separated glass plates for observation. Seeing a yellow, viscous secretion (which he found to be neutral or weakly acidic) produced from the gland, he proposed two alternative hypotheses about its function. First, he thought the secretion might enable the larva to obtain a grip with the anal pseudopod on the substrate, thus assisting locomotion. Second, and more likely because of its acidity, he thought the secretion might serve a defensive function against predators.



Apparently unaware of the work by Brass (1914), Wasmann (1915) sectioned larvae of *Lomechusoides* and discovered a median gland similar to that of *Leptusa* but lacking a posterior protuberance. He illustrated it and suggested an exudatory function but did not speculate on its purpose. However, this work was a stimulus for further studies on myrmecophilous and termitophilous Aleocharinae. Silvestri (1921) speculated that the substance produced by the median gland of *Termitoptochus* larvae probably is consumed by termites which in turn nourish the beetle larvae. Hölldobler (1967) working on *Lomechusa* and *Lomechusoides* larvae, and Hölldobler *et al.* (1982) working on *Pella* larvae, found circumstantial evidence to suggest that the secretion prompts adoption behavior in the host ants.

Kemner (1918) examined larvae of several aleocharine genera and reported three conditions of the gland. In larvae of *Leptusa*, *Bolitochara*, *Homalota*, *Anomognathus* and *Autalia*, the gland is well developed, protuberant and overhangs segment IX. In larvae of *Placusa* and *Haploglossa*, the gland is well developed but lacks the posterior protuberance. In larvae of *Thamiaraea*, *Atheta*, *Dinaraea*, *Falagria* and *Drusilla*, the gland is more feebly developed and lacks a reservoir. Kemner (1918) believed the gland to have a defensive function and discounted the possibility of a locomotory function. Later, Kemner (1925a) described larvae of *Diglotia* and (1926) of *Aleochara* without reference to a median gland, seemingly implying its absence and (1925b) reported presence of a median gland in larvae of *Affinoptochus*. The Brass-Kemner hypothesis that the function of the median gland is defensive appears subsequently to have been ignored until Badgley and Fleschner (1956) suggested a defensive function for the gland of *Oligota* larvae, a suggestion reiterated by Moore *et al.* (1975) and Moore (1978).

Verhoeff (1919) was the third author to describe the median gland of *Leptusa* larvae, although he made no reference to the work by Kemner (1918). He presented a reasoned argument refuting the suggestion by Brass (1914) of a possible locomotory function of the gland. He did not mention Brass' preferred hypothesis of a defensive function but produced a wholly new hypothesis. Observing cocoon-spinning, he assumed the median gland was the source of the threads of silk. The hypothesis of the median gland as a sericigenic gland was adopted by subsequent authors including Paulian (1941) and Beaver (1967), whereas Chamberlin and Ferris (1929) seem to have arrived at the same hypothesis independently.

Presence of a protuberance of abdominal segment VIII has been noted in various other aleocharine larvae whose external structures have been described for purely taxonomic purposes (Table 1).

### COCOON-SPINNING BY PREPUPAE OF ALEOCHARINAE

The first account of an aleocharine cocoon appears to have been an observation by Fauvel (1862) on *Leptusa*. Further records were added over the following decades (Table 2).

The definition of the material as silk does not imply that it is of the same chemical nature as in either the silkworm *Bombyx* or in spiders, but rather follows the broad definition used by Rudall and Kenchington (1971) of a fibrous material insoluble in water, whose predominant polymeric substance is proteinaceous, or polysaccharide or even hydrocarbon.

Verhoeff (1919) observed the process in a *Leptusa* prepupa. The production of silken threads was accompanied by to-and-fro movement of the abdominal apex, thus excluding the possibility of origin of the silk from modified salivary glands. Whereas Verhoeff (1919)

associated silk production with the median gland and hardening of the silk with a mucous secretion from the anus, Kemner (1926) mentioned the production of a silken cocoon by *Aleochara* prepupae of two species which seem to lack a median gland, thus substantiating his earlier (1918) hypothesis that silk issues from the anus. Badgley and Fleschner (1956) observed cocoon-spinning by an *Oligota* prepupa; since these authors had identified the median gland as a defensive gland, their implication of sericigenic glands "at the tip of the abdomen" excludes the median gland. Observations by Ashe (1982) on cocoon-spinning by *Gyrophaena* again point to silk production from the anus. Further, since dissections and histological sections of aleocharine larvae by Brass (1914), Wasmann (1915), Kemner (1918), Verhoeff (1919), Warren (1920) and Hölldobler (1967) produced no evidence of any other large abdominal glands apart from the median gland, then silk must issue from the anus and must be produced by some part of the digestive system.

Kemner's (1918) hypothesis that the Malpighian tubules are the site of silk production rests partly on his evidence of the swollen state of the Malpighian tubules in prepupal aleocharines he examined, and partly on his analogy of Malpighian tubules as the source of silk in Neuroptera and various other families of Coleoptera. There remains the possibility that the peritrophic membrane is the source of the silk as reported for prepupae of some other families of Coleoptera (e.g. Kenchington 1976), with the Malpighian tubules as source of a nitrogenous cement or hardening agent.

Many, if not all, *Aleochara* larvae are parasitoidal inside dipterous puparia. Whereas some of these larvae emerge from the host puparium to pupate and produce a silken cocoon, others pupate inside the host puparium and do not spin a cocoon (Kemner 1926, Fuldner 1960, Peschke and Fuldner 1977). At least some of the latter produce a nitrogenous cement in the Malpighian tubules, secreted into a widening of the hind gut, then smeared over the inner surface of the excavated host puparium to form a pupal cell (Fuldner 1960). This phenomenon could be expanded into a unifying hypothesis: Malpighian tubules being the source of the cement could explain their swollen state in the *Leptusa* prepupae observed by Kemner (1918) and the mucus secreted from the anus of *Leptusa* prepupae observed by Verhoeff (1919). The ability to spin a silken cocoon occurs in prepupae of some *Aleochara* but could have been lost from those *Aleochara* which pupate inside the host puparium as an adaptation to endoparasitoidal existence. The source of the silk in all cocoon-spinning aleocharines could then be the peritrophic membrane.

All knowledge of aleocharine cocoons is based on observations of members of relatively more derived tribes. The need is now for studies of members of the less derived tribes Gymnusini, Deinopsini, Myllaenini and Pronomaeini. Such studies will determine whether cocoon-spinning is characteristic of all aleocharine prepupae or whether it evolved within various lineages of Aleocharinae. The Trichopseniinae have been considered a tribe of Aleocharinae by some authors but not others, so the question of ability of their prepupae to spin cocoons is pertinent.

#### COCOON-SPINNING BY PREPUPAE OF OTHER STAPHYLINIDS

Schlick (1894), Kryger (1915), Blair (1917), Welch (1965) and Weinreich (1968) observed that larvae, or more properly prepupae, of *Stenus* species spin a silken cocoon before pupation. Bro Larsen (1959) stated that most *Stenus* prepupae make a loosely woven cocoon, but some (e.g. *S. cicindeloides* (Schaller)) make a tightly woven one. Jenkins (1958) observed spinning behavior in *Dianous coerulescens* Gyllenhal and dissected larvae to locate the silk glands. He

used histological techniques to demonstrate the presence of silk in them. These glands are elongate and extend through five abdominal segments; their openings are on tergum IX and they form the twelfth of a series of paired openings (Fig. 1C) of which 1-11 are those of the segmental glands. It is highly likely that silk production in *Stenus* is of the same origin, despite a conflicting observation by Weinreich (1968) of silk issuing from the anus, so that this method of silk production is characteristic of the subfamily Steninae.

In the Paederinae, larvae of *Astenus procerus* (Gravenhorst) and of an unidentified *Astenus* were reported to build silken cocoons by Peyerimhoff (1899) and Kemner (1925b) respectively, but these authors did not investigate the origin of the silk. In dissections of alcohol-preserved *Astenus* larvae collected with the adults in Florida and whose generic identity was confirmed using keys by Kasule (1970), we found no trace of glands such as described for *Dianous* by Jenkins (1958). Silk production seems to have been reported in no other genus of Paederinae. If the above accounts are accurate and silk production is characteristic of *Astenus*, it seems not to be of the same origin as in stenine prepupae.

Ability to spin silk by aleocharine and stenine prepupae holds no implications for a close relationship of these two subfamilies for the silk is of different origin and the ability to spin is a convergence. However, possibly the origin of silk in prepupae of *Astenus* and of aleocharines may be the same; further, it may be that the origin of the nitrogenous cement used for hardening of the wall of earthen pupation cells of some staphylinines (e.g. Paulian 1941) is produced by the Malpighian tubules as in *Aleochara* prepupae. Study of silk production throws no more light on relationships of Steninae than did a recent study (Frank 1982) of host-parasite relationships. Silk production is yet unreported for prepupae of subfamilies of Staphylinidae other than those of Aleocharinae, Paederinae and Steninae.

## GLANDS OF STAPHYLINID LARVAE AND ALEOCHARINE ADULTS

The openings of the silk glands of *Dianous* larvae appear to be the openings of the modified 12th pair of segmental glands (Jenkins 1958 and Fig. 1C). The function of the remaining pairs of glands, which are very small in relation to the silk glands, was suggested by Jenkins (1958) to be defensive. The segmental glands of staphylinines (Fig. 1A) and oxytelines (Fig. 1B) are not modified into silk glands.

Abdominal segment IX of aleocharines (Fig. 1D) lacks segmental glands and segment VIII contains segmental glands as well as the median gland (Hölldobler 1967). The median gland consists of two pairs of glands opening into a common reservoir. Are the two pairs of glands those of segment IX which migrated anteriorly to segment VIII? Since segment IX of some other staphylinids (Fig. 1A, B) contains two pairs of glands, one pair of which may have migrated from segment X, the question is not too far-fetched. Then, if Jenkins' (1958) suggestion of a defensive function of the segmental glands is correct, the median gland may retain its original function. If Kemner (1918) was correct that the median gland characteristic of *Thamiaraea*, *Atheta*, *Dinaraea*, *Falagria* and *Drusilla* lacks a reservoir but has a single dorsal opening, then the evolutionary process should have consisted of: 1) anterior migration of the four separate glands from segment IX; 2) their unification with a common duct; and 3) the development of an enlarged reservoir.

Unfortunately, the true function of the segmental glands is unclear. Georgevitsch (1898) likened them to the nephridial excretory system of annelids. Verhoeff (1919) named them "Gelenkdrüsen", thus imputing lubricative properties to their secretion in connection with

	head	thorax			abdomen									
		i	ii	iii	i	ii	iii	iv	v	vi	vii	viii	ix	x
A	o	o	o	o	o	o	o	o	o	o	o	o	o	
	o	o	o	o	o	o	o	o	o	o	o	o	o	
B				o	o	o	o	o	o	o	o	o	o	
				o	o	o	o	o	o	o	o	o	o	
C		o	o	o	o	o	o	o	o	o	o	s		
		o	o	o	o	o	o	o	o	o	o	s		
D	o	o	o	o	o	o	o	o	o	o	o	m		
	o	o	o	o	o	o	o	o	o	o	o	o		

FIG. 1. Schematic diagrams of the distribution of exocrine glands in staphylinid larvae: A, *Ocypus* (after Georgevitch, 1898); B, *Anotylus* (after Verhoeff 1919); C, *Dianous* (after Jenkins 1958); D, *Lomechusa* and *Lomechusoides* (after Hölldobler 1967). Roman numerals indicate body segments, O = segmental glands, M = median gland, S = sericigenic gland.

articulation of sclerites. Jenkins (1958) guessed they have a defensive function. Hölldobler (1967) reported that their secretion in the myrmecophilous genera *Lomechusa* and *Lomechusoides* caused ant hosts to groom the beetle larvae. None of these hypotheses can be discounted at present and new studies are desirable to attempt to arrive at a unifying hypothesis.

Glandular systems of adult aleocharines have been studied more thoroughly than those of larvae and show suggestive parallels between adult and larval systems. Secretion of mucoproteins to lubricate articulations between sclerites by the primary glandular system of adults (Pasteels 1968, Araujo 1978) lends support to Verhoeff's (1919) idea of the general function of segmental glands of larvae. There is also a possibility that some of the secretions have anti-fungal properties (Frank 1982, Lawrence and Newton 1982). Adults possess a large tergal gland having paired gland clusters in abdominal segment VII but a reservoir in segment VI and with proven defensive function (Pasteels 1968). This is extraordinarily analogous to the median gland of larvae in both structure and function. The tergal gland was reported by Jordan (1913) and Pasteels (1968) to occur in adults of all aleocharine genera examined, belonging to free-living as well as myrmecophilous and termitophilous aleocharines of the tribes Oxypodini, Callicerini, Aleocharini, Falagriini, Myrmedoniini, Bolitocharini, Phytosini, Autaliini and Oligotini. It occurs in adults of Corotocini, Termitonannini and Termitohospitini (Pasteels 1969). It is present in some pygostenine adults, but is reduced or modified in, or lost from other members of this tribe and in termitophilous members of several tribes (Pasteels 1969, Shower and Kistner 1977, Kistner 1979). The earlier findings led Pasteels (1968) to conclude that it probably is present in all aleocharine adults. Unfortunately, no members of the plesiomorphic tribes Gymnusini, Deinopsini, Myllaenini and Pronomaeini had been included in these surveys. Therefore the state of phylogenetic knowledge rests on little better inclusiveness than that of

the tribal distribution of the larval median gland (Table 2) or cocoon-spinning (Table 1). Further, trichopseniine adults were reported to lack the tergal gland (Pasteels and Kistner 1971) just as their larvae lack the median gland (Kistner and Howard 1980).

Finally, it is apparent that the tergal gland of adults of different tribes, genera and species produces different chemicals (e.g., Brand *et al.* 1973, Peschke and Metzler 1982), so there is no conflict in the assumptions that what may be entirely or mainly defensive secretions in free-living species may have special functions in myrmecophilous and termitophilous species. It is not unreasonable to suggest that the secretions of the median gland of larvae act similarly, as defensive secretions in some species and with special functions in myrmecophilous and termitophilous species.

## CLASSIFICATION OF ALEOCHARINAE

Tribal classification of Aleocharinae is unsettled. Hammond's (1975) suspicion that the subfamily may contain as many as 100,000 species makes a satisfactory higher classification a matter of some urgency. The traditional arrangement is exemplified by Lohse (1974). Hypocyphtinae are treated as a subfamily separate from Aleocharinae, and the tribes of Aleocharinae arranged in linear order from Deinopsini, Gymnusini and Myllaenini through Bolitocharini to Oxypodini and Aleocharini.

Hammond (1975) pointed out a number of plesiomorphic character states of Deinopsini and Gymnusini and included Hypocyphtini and Trichopseniini within Aleocharinae. Seevers (1978): 1) considered the members of Hypocyphtini to belong to Aleocharinae, but included them in Oligotini; 2) maintained the distinction between Trichopseniinae and Aleocharinae mainly because the hind coxae are fused to the metasternum in adults of the former; 3) recognized that adults of Deinopsini-Gymnusini-Myllaenini are generalized in structure, but nevertheless placed them near the end of his linear arrangement; 4) criticized the traditional arrangement of tribes, pointing out its artificiality in placing the generalized Oxypodini and Aleocharini near the end of the list, and called for reversion to a more natural classification similar to that by Ganglbauer (1895). This arrangement began with Oxypodini and progressed through Aleocharini and Myrmedoniini, with Bolitocharini, Phytosini and Oligotini near its end (Seevers 1978).

Investigation of phylogeny in Aleocharini will be aided by the identification of derived character states common to groups of tribes. To date, structures of aleocharine larvae seem not to have been used for this purpose despite numerous descriptions scattered in the literature.

Characterization of the Aleocharinae in terms of presence of a tergal gland in the adult, cocoon-spinning ability of the prepupa, and occurrence and condition of a median gland in the larva is hampered by lack of knowledge of the tribes Gymnusini, Deinopsini, Myllaenini and Pronomacini. Hammond (1975) considered Gymnusini-Deinopsini as a sister taxon to all remaining tribes of Aleocharinae. Klimaszewski (1982) considered Gymnusini-Deinopsini-Myllaenini a monophyletic group. Seevers (1978) also included Pronomacini in this group.

Seevers (1978) considered Aleocharini and Hoplandriini distinct tribes forming a single phyletic line. Adults of both tribes have a tergal gland. The prepupa of some species has the ability to spin a cocoon and it is conceivable that some species have lost the ability in adaptation to an endoparasitoid existence. Neither Kemner (1918, 1926) nor subsequent authors have reported median glands in *Aleochara* larvae. Whether lack of the median gland in Aleocharini is a plesiomorphic character state must yet be considered uncertain.

Diglottini have been considered by some authors (e.g., Seevers 1978, Klimaszewski 1982) as possibly related to Phytosini (see below), yet Kemner (1925a) made no mention of a median gland or cocoon-spinning in *Diglotta* prepupae nor has a tergal gland in the adult been revealed. Since members of Phytosini (see below) possess all 3 characteristics, the relationships of Diglottini still remain obscure.

Falagriini and Callicerini are reported to possess a tergal gland in the adult, silk-spinning ability in the prepupa, and a feebly developed median gland without reservoir in the larva. However, in larvae questionably attributed to *Alianta* (Callicerini), the median gland has been reported to be protuberant. These two tribes seem to exhibit a plesiomorphic condition of the median gland which, in the tribes mentioned below, is either better developed or there is reason to believe its reduction is an adaptation to a specialized way of life.

Oxypodini and Myrmedoniini, both *sensu* Seevers (1978), have a tergal gland in the adult, silk-spinning ability in the prepupa, and a median gland with large reservoir in the larva. These characteristics are shared with those corotocines and drepanoxenines in which the tergal gland has not been modified or lost secondarily. Unlike its condition in the tribes mentioned below, the median gland is not protuberant. The two known exceptions to these generalizations bear consideration. *Phloeopora* larvae (Oxypodini) have a protuberant gland. Since adult *Phloeopora* possess widely separated mesocoxae although the tribe is characterized as having narrowly separated mesocoxae (Seevers 1978), *Phloeopora* may be misplaced in the Oxypodini. *Drusilla* larvae (Myrmedoniini) seem to lack a median gland reservoir; if so, it could be a secondary loss in this myrmecophilous genus just as the tergal gland in some myrmecophilous and termitophilous species has been reduced, modified or lost.

Bolitocharini, Autaliini, Phytosini, Oligotini and Hypocyphptini were considered by Seevers (1978) to form a related group of tribes. The adult has a tergal gland (not known for Hypocyphptini), the prepupa has the ability to spin a silken cocoon (not known for Autaliini and Hypocyphptini), and the median gland of the larva is prominent and protuberant. This group of tribes has the most highly developed median gland structure; in *Oligota* larvae the gland has been reported to be operculate (Badgley and Fleschner 1956, Moore *et al.* 1975) and this may represent a further structural development. The only known exception is *Placusa* (Bolitocharini) whose larvae seem to lack the glandular protuberance; if so it could represent a secondary loss or the genus is incorrectly assigned.

It is difficult to determine the relationships of Trichopseniinae to any of the above groups of tribes. The adults lack a tergal gland (Pasteels and Kistner 1971) but this could be a secondary loss as in other termitophilous aleocharines; a lamellar process of the metacoxa is more highly developed than in oligotines and hypocyphptines (Seevers 1978). The mandible of the larva has a more pronounced median tooth (Kistner and Howard 1980) than is known in other aleocharines. The abdomen has a structure resembling the protuberant median gland of larvae of the Bolitocharini-Autaliini-Phytosini-Oligotini-Hypocyphptini, but no orifice has been discovered (Kistner and Howard 1980) so the homologies of this structure are unclear.

## CONCLUSION

Present knowledge suggests that cocoon-spinning ability of prepupae and presence of a tergal gland in adults are characteristic of Aleocharinae except in those groups where the attributes have been lost secondarily. It is not known whether the possibly monophyletic and probably generalized Gymnusini-Deinopsini-Myllaenini-Pronomacini possess these attributes,

so examination of members of these tribes will elucidate phylogeny.

The median gland of aleocharine larvae is most highly developed within the more-derived tribes Bolitocharini-Autaliini-Phytosini-Oligotini-Hypocyphtini. Its less developed condition within the less derived tribes suggests the gland evolved within Aleocharinae, shows a phyletic sequence of development among tribes, and may not be present within all tribes. Its condition is unknown for larvae of the less derived tribes Gymnusini-Deinopsini-Myllaenini-Pronomaeini. The median gland is feebly developed within larvae of Falagriini-Callicerini and better developed within larvae of Oxypodini-Corotocini-Drepanoxenini-Myrmedoniini. Aleocharini, in whose larvae the gland has not yet been revealed, may be less derived than Oxypodini. A detailed histological survey of this structure within larvae of Aleocharinae should yield a wealth of phylogenetic information.

### ACKNOWLEDGMENTS

We are most grateful to Hedvig Evans (Fort Pierce) for an exact translation of parts of Bro Larsen's paper from Danish and to June Jacobson (Gainesville) for providing photocopies of some of the literature cited. We are indebted to W. Topp (Bayreuth) for supplying information on larvae of *Cordalia* and *Falagria*, and to M. Sörensson (Lund) for supplying a copy of Kemner's (1918) work. L. H. Herman (New York) and J. Klimaszewski (Ottawa) kindly reviewed the manuscript and made helpful comments.

### LITERATURE CITED

- Araujo, J. 1978. Anatomie comparée des systèmes glandulaires de défense chimique des Staphylinidae. Archives de Biologie (Bruxelles) 89: 217–250.
- Arnett, R. H. 1961. The beetles of the United States (A manual for identification). Pt. II, fasc. 10–24. Catholic Univ. America Press, Washington, D.C.
- Ashe, J. S. 1981. Studies of the life history and habits of *Phanerota fasciata* Say (Coleoptera: Staphylinidae: Aleocharinae) with notes on the mushroom as a habitat and descriptions of the immature stages. Coleopterists Bulletin 35: 83–96.
- Ashe, J. S. 1982. Construction of pupal cells by larvae of Aleocharinae (Coleoptera: Staphylinidae). Coleopterists Bulletin 35: 341–343.
- Azab, A. K., M. S. F. Tawfik and K. T. Awadallah. 1963. Insect enemies of common flies in Giza region. Bulletin de la Société Entomologique d'Egypte 47: 277–286.
- Badgley, M. E. and C. A. Fleschner. 1965. Biology of *Oligota oviformis* Casey. Annals of the Entomological Society of America 49: 501–502.
- Beaver, R. A. 1967. Notes on the fauna associated with elm bark beetles in Wytham Wood, Berks. – I. Coleoptera. Entomologist's Monthly Magazine 102: 163–170.
- Beier, M. and H. Strouhal. 1928. Käferlarven und Käferpuppen aus Maulwurfsnestern. Zeitschrift für Wissenschaftliche Insektenbiologie 23: 1–34, pl. 1–4.
- Blair, K. G. 1917. A note on the biology of *Stenus similis* Herbst. Entomologist's Monthly Magazine 53: 175.
- Bøving, A. G. and F. C. Craighead. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana (new series) 11: 1–351.
- Brand, M., M. S. Blum, H. M. Fales and J. M. Pasteels. 1973. The chemistry of the defensive secretion of the beetle *Drusilla canaliculata*. Journal of Insect Physiology. 19: 369–382.

- Brass, P. 1914. Das 10. Abdominalsegment der Käferlarven als Bewegungsorgan. *Zoologische Jahrbücher Abteilung für Systematik* 37: 65–122, 4–7.
- Bro Larsen, E. 1959. Traek af steninerne Biologi. *Notulae Entomologicae* 39: 87–88.
- Cerruti, M. 1952. Descrizione delle larve di due stafilinidi dorilofili dell'Africa orientale (Col., Staphylinidae). *Rivista di Biologia Coloniale* 12:49–56.
- Chamberlin, J. S. and G. F. Ferris. 1929. On *Liparocephalus* and allied genera. *Pan-Pacific Entomologist* 5: 137–143, 153–162.
- Coquillett, D. W. 1891. Another parasitic rove beetle. *Insect Life* 3: 318–319.
- Cottier, W. 1932. A study of the insect fauna of swede turnips infected with dry-rot. *New Zealand Journal of Science and Technology* 14: 142–145.
- Dajoz, R. 1960. Description de la larve de *Leptusa doderoi* Bernhauer (Col. Staphylinidae). *Bulletin de la Société Entomologique de France* 65: 132–134.
- Dobson, R. M. 1961. Observations on natural mortality, parasites and predators of wheat bulb fly, *Leptohylemyia coarctata* (Fall.). *Bulletin of Entomological Research* 52: 281–291.
- Falcoz, L. 1919. Description de la larve de *Microglossa pulla* Gyll. (Col., Staphylinidae). *Bulletin de la Société Entomologique de France* (1919): 296–301.
- Fauvel, A. 1862. Notice sur quelques aleochariens nouveaux ou peu connus et description de larves de *Phytosus* et *Leptusa*. *Annales de la Société Entomologique de France* (série 4) 2: 81–94, pl. 2.
- Fauvel, A. 1875. Faune Gallo-Rhénane ou species des insectes qui habitent la France, la Belgique, la Hollande, le Luxembourg, la Prusse Rhénane, le Nassau et le Valais. Fauvel; Caen, Vol. 3, part 6, pp. 545–738.
- Frank, J. H. 1982. The parasites of the Staphylinidae (Coleoptera). A contribution towards an encyclopedia of the Staphylinidae. University of Florida, Agricultural Experiment Station Bulletin 824: i–vii, 1–118.
- Fuldner, D. 1960. Beiträge zur Morphologie und Biologie von *Aleochara bilineata* Gyll. und *A. bipustulata* L. (Coleoptera: Staphylinidae). *Zeitschrift für Morphologie und Ökologie der Tiere*. 49: 312–386.
- Ganglbauer, L. 1895. Die Käfer von Mitteleuropa. Die Käfer der österreichisch-ungarischen Monarchie, Deutschlands, der Schweiz, sowie des französischen und italienischen Alpengebietes. Bd. 2. Familienreihe Staphylinoidea. 1. Theil: Staphylinidae, Pselaphidae. Carl Gerold's Sohn; Vienna, 880 pp.
- Georgevitch, J. 1898. Die Segmentaldrüsen von *Ocypus*. *Zoologischer Anzeiger* (1898): 256–261.
- Hammond, P. M. 1975. The phylogeny of a remarkable new genus and species of gymnosine staphylinid (Coleoptera) from the Auckland Islands. *Journal of Entomology* (B) 44: 153–173.
- Heim de Balsac, H. 1938. Commensalisme ornithophile de coléoptères staphylinides; son déterminisme par exigences thermiques de maturation des gonades. *Compte Rendu de l'Académie des Sciences, France* 207: 644–646.
- Hölldobler, B. 1967. Die Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen. I. Das Gastverhältnis der *Atemeles* und *Lomechusa* Larven (Col. Staphylinidae) zu *Formica* (Hym. Formicidae). *Zeitschrift für Vergleichende Physiologie* 56: 1–21.
- Hölldobler, B., M. Möglich, and U. Maschwitz. 1982. Myrmecophilic relationship of *Pella* (Coleoptera: Staphylinidae) to *Lasius fuliginosus* (Hymenoptera: Formicidae). *Psyche* 88: 347–374.



- Jenkins, M. F. 1958. Cocoon building and the production of silk by the mature larva of *Dianous coerulescens* Gyllenhal (Coleoptera: Staphylinidae). Transactions of the Royal Entomological Society of London 110: 287–301.
- Jordan, K. H. C. 1913. Zur Morphologie und Biologie der myrmecophilen Gattungen *Lomechusa* und *Atemeles* und einiger verwandter Formen. Zeitschrift für Wissenschaftliche Zoologie 107: 346–386.
- Joy, N. H. 1906. Coleoptera occurring in the nests of mammals and birds. Entomologist's Monthly Magazine 42: 198–202, 237–243.
- Kasule, F. K. 1966. The subfamilies of the larvae of Staphylinidae with keys to the larvae of the British genera of Steninae and Proteininae. Transactions of the Royal Entomological Society of London 118: 261–283.
- Kasule, F. K. 1970. The larvae of Paederinae and Staphylininae (Coleoptera: Staphylinidae) with keys to the known British genera. Transactions of the Royal Entomological Society of London 122: 49–80.
- Kemner, N. A. 1918. Vergleichende Studien über das Analsegment und das Pygopodium einiger Koleopterenlarven. (Akademische Abhandlung, Univ. Lund). Wretman's Boktryckeri; Uppsala, 104 pp.
- Kemner, N. A. 1925a. Zur Kenntnis der Staphyliniden-Larven. I. Die Larven der Tribus Proteinini und Diglossini. Entomologisk Tidskrift 46: 61–77, pl. 1–2.
- Kemner, N. A. 1925b. Über die Zucht von einer "Larva eutermia" aus Java und das Ausschlüpfen aus derselben der physogastrischen Aleocharide *Affinoptochus exclusus* n.g., n.sp. Arkiv för Zoologi 18 (A,10): 1–24, pl. 1–3.
- Kemner, N. A. 1926. Zur Kenntnis der Staphyliniden-Larven. II. Die Lebensweise und parasitische Entwicklung der echten Aleochariden. Entomologisk Tidskrift 47: 133–170, pl. 7–10.
- Kenchington, W. 1976. Adaptation of insect peritrophic membranes to form cocoon fabrics (pp. 497–513) in H. R. Hepburn (ed.) The insect integument. Elsevier; New York, xix + 571 pp.
- Kistner, D. H. 1976. Revision and redescription of the genus *Goniusa* Casey with a larval description and ant host records (Coleoptera: Staphylinidae). Sociobiology 2: 83–95.
- Kistner, D.H. 1979. Social and evolutionary significance of social insect symbionts (chapter 8, pp. 339–413) in H. R. Herman (ed.) Social insects. Academic Press; New York, Vol. 1, xv + 437 pp.
- Kistner, D.H. and R. W. Howard. 1980. First report of larval and pupal Trichopseniinae: external morphology, taxonomy and behavior (Coleoptera: Staphylinidae). Sociobiology 5: 3–20.
- Kistner, D. H. and J. A. L. Watson. 1972. A new tribe of termitophilous Aleocharinae (Coleoptera: Staphylinidae) from Australia. Australian Journal of Zoology, Supplemental Series 17: 1–24.
- Klimaszewski, J. 1982. A redefinition of Myllaenini Ganglbauer and redescriptions of *Camacopalpus* Motschulsky and *Polypea* Fauvel (Coleoptera: Staphylinidae). Canadian Entomologist 114: 411–429.
- Kryger, J. P. 1915. Biologiske Oplysninger om nogle nye eller sjældne Billelarver. Entomologiske Meddelelser 10: 172–179.
- Kryger, J. P. and H. P. S. Sønderup. 1940. Biologiske Iagttagelser over 200 Arter af danske Billelarver. Entomologiske Meddelelser 22: 57–136.
- Lawrence, J. F. and A. F. Newton. 1982. Evolution and classification of beetles. Annual

Review of Ecology and Systematics 13: 261–290.

- Lohse, G. A. 1974. Staphylinidae II (Hypocyphinae und Aleocharinae) Pselaphidae. (Bd. 5, 381 pp.) in H. Freude, K. W. Harde and G. A. Lohse (eds.) Die Käfer Mitteleuropas. Goecke and Evers; Krefeld.
- Moore, I. 1956. Notes on some intertidal Coleoptera with descriptions of the early stages (Carabidae, Staphylinidae, Malachiidae). Transactions of the San Diego Society of Natural History 12: 207–230, pl. 14–17.
- Moore, I. 1977. The larva of *Rothium sonorensis* Moore and Legner, with a key to the known larvae of the genera of the marine Bolitocharini (Coleoptera: Staphylinidae). Psyche 83: 262–266.
- Moore, I. 1978. Usefulness of larval osmeteria in determining natural classification in Aleocharinae (Coleoptera: Staphylinidae). Entomological News 89: 245–246.
- Moore, I. 1979. Notes of *Bryothinusa* with description of the larva of *B. catalinae* Casey (Coleoptera: Staphylinidae). Psyche 85: 183–189.
- Moore, I., E. F. Legner and M. E. Badgley. 1975. Description of the developmental stages of the mite predator *Oligota oviformis* Casey with notes on the osmeterium and its glands (Coleoptera: Staphylinidae). Psyche 82: 181–188.
- Nuorteva, M. 1956. Über die Fichtenstamm-Bastkäfer *Hylurgops palliatus* Gyll., und seine Insektenfeinde. Acta Entomologica Fennica 13: 1–118.
- Pasteels, J. M. 1968. Le système glandulaire tégumentaire des Aleocharinae (Coleoptera, Staphylinidae) et son evolution chez les espèces termitophiles du genre *Termitella*. Archives de Biologie (Liège) 79: 381–469.
- Pasteels, J. M. 1969. Les glandes tégumentaires des staphylins termitophiles. III. Les Aleocharinae des genres *Termitopullus* (Corotocini, Corotocina), *Perinthodes*, *Catalina* (Termitonannini, Perinthina), *Termitusa* (Termitohospitini, Termitusina). Insectes Sociaux 15: 337–358.
- Pasteels, J. M. and D. H. Kistner. 1971. Revision of the termitophilous subfamily Trichopseniinae (Coleoptera: Staphylinidae). II. The remainder of the genera with a representational study of the gland systems and a discussion of their relationships. Miscellaneous Publications of the Entomological Society of America 7 (4): 349–399.
- Paulian, R. 1942. Les premiers états des Staphylinoidea (Coleoptera). Etude de morphologie comparée. Mémoires du Museum National d'Histoire Naturelle, Paris 15: 1–361.
- Paulian, R. 1948. Observations sur les coléoptères commensaux d'*Anomma nigricans* en Cote d'Ivoire. Annales des Sciences Naturelles, Zoologie (série 11) 10: 79–102.
- Perris, E. 1853. Histoire des insectes du pin maritime. Suite. Annales de la Société Entomologique de France (série 3) 1: 555–579, pl. 17.
- Peschke, K. and D. Fuldner. 1977. Übersicht und neue Untersuchungen zur Lebensweise der parasitoiden Aleocharinae (Coleoptera: Staphylinidae). Zoologische Jahrbücher Abteilung für Systematik 104: 242–262.
- Peschke, K. and M. Metzler. 1982. Defensive and pheromonal secretion of the tergal gland of *Aleochara curtula*. I. The chemical composition. Journal of Chemical Ecology 8: 773–783.
- Peyerimhoff, P. de 1899. Note sur la larve myrmecophile d'*Astenus filiformis* Latr. (Col.). Bulletin de la Société Entomologique de France (1899): 287–289.
- Rey, C. 1887. Essai d'études sur certaines larves de coléoptères et descriptions de quelques espèces inédites ou peu connues. André; Beaune, 126 pp. 2 pl.
- Rudall, K. M. and W. Kenchington. 1971. Arthropod silks: the problem of fibrous proteins in

- animal tissues. *Annual Review of Entomology* 16:73–96.
- Scheerpeltz, O. 1958. Neue Staphyliniden aus Höhlen in Gabon und im französischen Kongo (Col.). *Revue Suisse de Zoologie* 65: 825–842.
- Schlick, W. 1894. Biologische Bidrag. Coleoptera. *Entomologische Mittheilungen* 4: 290–311.
- Schlick, W. 1899. Biologische Bidrag. Coleoptera 3. *Entomologische Mittheilungen* 49–66.
- Seevers, C. H. 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera: Staphylinidae). *Fieldiana Zoology* 71: i–vi, 1–289.
- Shower, J. A. and D. H. Kistner. 1977. The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae). Section 4: Glandular anatomy of the Pygostenini. *Sociobiology* 2: 305–326.
- Silvestri, F. 1921. Descrizione di alcuni Staphylinidae (Coleoptera) delle regioni orientale e australiana. *Bollettino del Laboratorio di Zoologia, Portici* 15: 3–23.
- Steel, W. O. 1964. Insects of Campbell Island. Coleoptera: Staphylinidae. *Pacific Insects Monograph* 7: 34–75.
- Tawfik, M. F. S., K. T. Awadallah, E. D. Ammar and S. M. Abul-Ela. 1976. The life-history of *Aleochara moesta* Gr., a natural enemy of houseflies in Egypt (Coleoptera: Staphylinidae). *Bulletin de la Société Entomologique d'Egypte* 60: 367–377.
- Topp, W. 1971. Zur Biologie und Larvalmorphologie von *Atheta sordida* Marsh. (Col., Staphylinidae). *Annales Entomologici Fennici* 37: 85–89.
- Topp, W. 1973. Über Entwicklung, Diapause und Larvalmorphologie der Staphyliniden *Aleochara moerens* Gyll. und *Bolitochara lunulata* Payk. in Nordfinland. *Annales Entomologici Fennici* 39: 145–152.
- Topp, W. 1975a. Morphologische Variabilität, Diapause und Entwicklung von *Atheta fungi* (Grav.) (Col., Staphylinidae). *Zoologische Jahrbücher Abteilung für Systematik* 102: 101–127.
- Topp, W. 1975b. Zur Larvalmorphologie der Athetae (Col., Staphylinidae). *Stuttgarter Beiträge zur Naturkunde (Serie A)* 268: 1–23.
- Topp, W. 1978. Bestimmungstabelle für die Larven der Staphylinidae (pp. 304–334) in B. Klausnitzer (ed.) *Ordnung Coleoptera (Larven)*. W. Junk; The Hague, vi + 378 pp.
- Verhoeff, K. W. 1919. Studien über die Organisation und Biologie der Staphylinidea. V. Zur Kenntnis der Oxyteliden-Larven. *Archiv für Naturgeschichte* 85 (A,6): 48–111, pl. 3–4.
- Warren, E. 1920. Observations on the comparative anatomy of the termitophilous aleocharine *Paracorotoca akermanni* (Warren). *Annals of the Natal Museum* 4: 297–366, pl. 16–21.
- Wasmann, E. 1890. Vergleichenden Studien über Ameisengäste und Termitengäste. *Tidschrift voor Entomologie* 33: 17–96, pl. 1.
- Wasmann, E. 1894. Zur Lebens- und Entwicklungsgeschichte von *Atemeles pubicollis* mit einem Nachtrag über *Atemeles emarginatus*. *Deutsche Entomologische Zeitschrift* (1894): 281–283.
- Wasmann, E. 1915. Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles* mit kritischen Bemerkungen über das echte Gastverhältnis. *Zeitschrift für Wissenschaftliche Zoologie* 114: 233–402, pl. 9–10.
- Watson, J. A. L. 1973. A further species of the termitophilous aleocharine *Drepanoxenus* (Coleoptera: Staphylinidae). *Journal of the Australian Entomological Society* 12: 233–235.
- Watson, J. A. L. 1979. *Drepanoxenus bos*, a new termitophilous aleocharine from northwestern Australia (Coleoptera: Staphylinidae). *Journal of the Australian Entomological Society* 18: 53–56.

- Watson, J. A. L. and D. H. Kistner. 1972. The glandular anatomy and biology of the termitophilous Australian aleocharine *Drepanoxenus* (Coleoptera: Staphylinidae). Australian Journal of Zoology 20: 341–358.
- Weinreich, E. 1968. Über den Klebfangapparat der Imagines von *Stenus* Latr. (Coleopt. Staphylinidae) mit einem Beitrag zur Kenntnis der Jugendstadien dieser Gattung. Zeitschrift für Morphologie der Tiere 62: 162–210.
- Welch, R. C. 1965. A description of the pupa and third instar larva of *Stenus canaliculatus* Gyll. (Col., Staphylinidae). Entomologist's Monthly Magazine 101: 246–250.
- White, E. B. and E. F. Legner. 1966. Notes on the life history of *Aleochara taeniata*, a staphylinid parasite of the house-fly, *Musca domestica*. Annals of the Entomological Society of America 59: 573–577.
- White, I. M. 1977. The larvae of some British species of *Gyrophana* Mannerheim (Coleoptera: Staphylinidae) with notes on the taxonomy and biology of the genus. Zoological Journal of the Linnean Society of London 60: 297–317.

Table 1. Four conditions of the median gland in aleocharine larvae as interpreted from the following sources: 1: Perris (1853), 2: Fauvel (1862), 3: Fauvel (1875), 4: Rey (1887), 5: Wasmann (1915), 6: Kemner (1918), 7: Falcoz (1919), 8: Verhoeff (1919), 9: Warren (1920), 10: Silvestri (1921), 11: Kemner (1925a), 12: Kemner (1925b), 13: Kemner (1926), 14: Beier and Strouhal (1928), 15: Chamberlin and Ferris (1929), 16: Bøving and Craighead (1931), 17: Paulian (1941), 18: Paulian (1948), 19: Cerruti (1952), 20: Badgley and Fleschner (1956), 21: Moore (1956), 22: Scheerpeltz (1958), 23: Dajoz (1960), 24: Fuldner (1960), 25: Steel (1964), 26: Kasule (1966), 27: Beaver (1967), 28: Hölldobler (1967), 29: Topp (1971), 30: Kistner and Watson (1972), 31: Watson and Kistner (1972), 32: Topp (1973), 33: Watson (1973), 34: Topp (1975a), 35: Topp (1975b), 36: Kistner (1976), 37: Moore (1977), 38: White (1977), 39: Topp (1978), 40: Moore (1979), 41: Watson (1979), 42: Kistner and Howard (1980), 43: Ashe (1981), 44: Topp (in litt.), 45: Hölldobler *et al.* (1982), 46: newly reported observation.

A. MEDIAN GLAND NOT REPORTED, HERE PRESUMED ABSENT

ALEOCHARINI: *Aleochara* 13, 24, 32, 39; DIGLOTTINI: *Diglotta* 11.

B. MEDIAN GLAND NOT REPORTED EXCEPT BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE AND THEN GLAND FOUND TO BE POORLY DEVELOPED AND WITHOUT RESERVOIR

FALAGRIINI: *Cordalia* 44, *Falagria* 6, 44; CALLICERINI: *Aloconota* 35, *Atheta* 1, 6, 8, 17, 22, 25, 34, 35, 39, *Dinaraea* 6, 35, *Geostiba* 35, *Nehemitropia* 28, 35, *Pachnida* 35, *Thamaraea* 6 (exception: *Alianta* 17, described as having a protuberant median gland as in condition D, but identified *ex societate imaginis*).

C. MEDIAN GLAND NOT REPORTED EXCEPT BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE AND THEN GLAND FOUND TO HAVE LARGE RESERVOIR

OXYPODINI: *Colle* 25, *Haploglossa* 6, 7, 17, *Ocalea* 17, *Ocyusa* 39, *Oxypoda* 14, 39, *Platyla* 4, *Tachyusa* 39 (exception: *Phloeopora* 1, 17, 46, has a protuberant median gland as in condition D); COROTOCINI: *Affinoptochus* 12, *Paracorotoca* 9, *Termitoptochus* 10, *Termitoptocinus* 10; DREPANOXENINI: *Drepanoxenus* 30, 31, 33, 41; MYRMEDONIINI: *Creodonia* 19, *Goniusa* 36, *Lomechusa* 28, *Lomechusoides* 5, 17, 28, *Pella* 45, *Smectonia* 19, *Zyras* 18, 39 (exception: *Drusilla* 6, 17, 39, seems to lack reservoir).

D. MEDIAN GLAND REPORTED AS PROMINENT AND PROTUBERANT, AS WELL (BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE) AS HAVING A LARGE RESERVOIR

BOLITOCHARINI: *Anomognathus* 6, 17, *Bolitochara* 6, 17, 26, 27, 32, *Cyphea* 3, *Gyrophaena* 4, 16, 17, 38, *Homalota* 6, 46, *Leptusa* 2, 6, 8, 23, 39, *Phanerota* 43 (exception: *Placusa* 1, 6, lacks the protuberance); AUTALIINI: *Autalia* 6; PHYTOSINI: *Amblopusa* 15, *Baeostethus* 25, *Bryothinusa* 40, *Diaulota* 21, *Halmaeus* 17, 25, *Liparocephalus* 15, 21, *Phytosus* 2, *Rothium* 37; OLIGOTINI: *Oligota* 4, 17, 20, 46; HYPOCYPHTINI: *Hypocyphtus* 26.

INCERTAE SEDIS

TRICHOPSENIINAE: *Trichopsenius* and *Xenistusa* 41 have a structure which resembles the protuberant condition D of the median gland but no orifice has been observed and the internal structure has not yet been examined.

Table 2. Aleocharine prepupae with cocoon-spinning ability according to: 1: Fauvel (1862), 2: Wasmann (1890), 3: Coquillett (1891), 4: Wasmann (1894), 5: Peyerimhoff (1899), 6: Schlick (1899), 7: Joy (1906), 8: Wasmann (1915), 9: Kemner (1918), 10: Verhoeff (1919), 11: Kemner (1925b), 12: Kemner (1926), 13: Chamberlin and Ferris (1929), 14: Cottier (1932), 15: de Balsac (1938), 16: Kryger and Sønderup (1940), 17: Paulian (1941), 18: Nuorteva (1956), 19: Badgley and Fleschner (1956), 20: Dobson (1961), 21: Azab *et al.* (1963), 22: White and Legner (1966), 23: Beaver (1967), 24: Topp (1971), 25: Topp (1973), 26: Tawfik *et al.* (1976), 27: Peschke and Fuldner (1977), 28: Ashe (1981), 29: Ashe (1982), 30: newly reported observation.

OXYPODINI: *Haploglossa pulla* (Gyllenhal) 7, 15; *Ocalea picata* (Stephens) 30

COROTOCINI: *Affinoptochus exclusus* Kemner 11.

CALLICERINI: *Atheta pseudocoriaria* Bernhauer 14, *Nehemitropia sordida* (Marsham) 24; *Thamiaraea cinnamomea* (Gravenhorst) 9.

ALEOCHARINI: *Aleochara curtula* (Goeze), *A. laevigata* Gyllenhal, *A. intricata* Mannerheim 12; *A. valida* LeConte 3; *A. inconspicua* Aubé 20; *A. moesta* Gravenhorst 21, 26; *A. taeniata* Erichson 22; *A. lata* Gravenhorst, *A. ripicola* Mulsant and Rey, *A. brevipennis* Gravenhorst, *A. puberula* Klug 27.

FALAGRIINI: *Cordalia* sp. 17.

MYRMEDONINI: *Lomechusa emarginata* (Paykull), *Lomechusoides strumosa* (Fabricius) 2, 4, 8; *Zyras cognatus* (Märkel) 6.

BOLITOCARINI: *Bolitochara obliqua* Erichson 23; *B. pulchra* (Gravenhorst) 25; *Euryusa sinuata* Erichson 16; *Gyrophana nana* Paykull 29; *Homalota ? lepidula* Casey 30; *Leptusa fumida* (Erichson) 1; *L. pulchella* (Mannerheim) 10; *Phanerota fasciata* Say 28; *Placusa* spp. 18.

PHYTOSINI: *Amblopusa brevipes* Casey, *Liparocephalus brevipennis* Mäklin 13.

OLIGOTINI: *Oligota flavicornis* (Boisduval and Lacordaire) 5; *O. oviformis* (Casey) 19; *O. minuta* Cameron 30.

Appendix 1. Synonymies. Names of some genera and species as used in the text differ from names as used by some authors cited. Synonyms are given in regular print and names used in the text are in *italics*.

Antarctophytosus Enderlein, 1909 = *Halmaeus* Kiesenwetter, 1877  
 Astenus filiformis (Latreille) = *Astenus procerus* (Gravenhorst)  
 Astilbus Dillwyn, 1829 = *Drusilla* Samouelle, 1819  
 Ateules Dillwyn, 1829 = *Lomechusa* Gravenhorst, 1806  
 Atheta sordida (Marsham) = *Nehemitropia sordida* (Marsham)  
 Bolitochara lunulata (Paykull) = *Bolitochara pulchra* (Gravenhorst)  
 Cardiola Mulsant & Rey, 1875 = *Cordalia* Jacobs, 1925  
*Creodonia* Wasmann has been raised to generic status  
 Diaulota brevipes (Casey) = *Amblopusa brevipes* Casey  
 Homalota celata Erichson = *Atheta celata* (Erichson)  
 Leptusa angusta Aubé = *Leptusa pulchella* (Mannerheim)  
 Lomechusa strumosa (Fabricius) = *Lomechusoides strumosa* (Fabricius)  
 Microglossa Stein, 1868 = *Haploglossa* Kraatz, 1856  
 Microglotta Kraatz, 1862 = *Haploglossa* Kraatz, 1856  
 Myrmedonia cognata Märkel = *Zyras cognatus* (Märkel)  
 Oxypoda moesta ERROR = *Aleochara moesta* Gravenhorst  
 Oxytelus tetracarinus (Block) = *Anotylus tetracarinus* (Block)  
 Sipalia circellaris (Gravenhorst) = *Geostiba circellaris* (Gravenhorst)  
 Sunius Erichson, 1839, nec Stephens, 1833 = *Astenus* Dejean, 1833  
 Thectura Thomson, 1859 = *Anomognathus* Solier, 1819





OBSERVATIONS ON THE POSSIBLE USE OF HABITAT CUES AND TOKEN STIMULI  
BY CATERPILLAR-HUNTING WASPS: *EUODYNERUS FORAMINATUS*  
(HYMENOPTERA, EUMENIDAE)

André L. Steiner  
Department of Zoology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E9

*Quaestiones Entomologicae*  
20: 25-33 1984

ABSTRACT

*Observations in the wild and a few tests in captivity gave indications that host-finding by the caterpillar-hunting eumenine wasp Euodynerus foraminatus depended mainly on two categories of stimuli: a) habitat cues such as green vegetation, leaves of trees, shrubs and plants, which were readily detected and investigated in captivity, even in the absence of prey or prey-related stimuli. The interest for such stimuli was short-lived, however, and they had no activating effects on the wasps. b) Token stimuli provided by the leaf-rolling microlepidopteran prey such as rolled leaves, frass, silk or odor left on leaves, produced longer lasting and activating effects. Upon contact with the antennae the wasps became very excited, chewed the stimuli and ran around wildly. Only the prey itself was stung, however. Parasitic Hymenoptera such as wood wasps (Siricidae), which hunt well concealed prey, also use habitat cues and/or token stimuli for host-finding. Some sphecids wasps that attack highly mobile and exposed prey such as common grasshoppers apparently do not use such cues.*

RÉSUMÉ

*Des observations sur le terrain et quelques tests de laboratoire semblent indiquer que certaines guêpes telles qu'Euodynerus foraminatus (Eumenidae) utilisent deux types de stimuli durant la chasse de leurs proies, des larves de Microlepidoptères qui vivent entre plusieurs feuilles enroulées: a) des stimuli reliés à l'habitat, par exemple des feuilles d'arbre, d'arbustes ou de plantes, qui sont visitées en captivité même en l'absence de proies ou de stimuli produits par ces dernières. Cependant l'intérêt suscité par de tels stimuli n'est que de très courte durée et aucun effet activateur n'est produit. b) Des stimuli-substituts de la proie tels que des feuilles enroulées, des excréments, fils de soie ou odeurs, laissés sur les feuilles par la proie suscitent un intérêt durable et produisent une vive excitation lorsque les antennes de la guêpe entrent en contact avec eux. La guêpe peut même mordre de tels objets mais elle ne piquera que la proie elle-même. Des guêpes parasites telles que les Siricidae, qui chassent des proies cachées, utilisent également des stimuli-substituts ou reliés à l'habitat. Ce n'est apparemment pas le cas pour des Sphégides qui s'attaquent à des proies très mobiles et exposées, telles que des criquets communs.*

INTRODUCTION

Some mammal-infesting ticks drop to the ground upon detection of butyric acid. Some leeches find their warm-blooded hosts on the basis of an increase in local temperature. Similarly, various parasitic Hymenoptera, such as braconid, ichneumonid or siricid wasps also use such "token" stimuli for host-finding or host-detection, for instance frass, symbiotic fungi or gland secretions left during oviposition by the host species, or even heat cues (see for instance Heatwole *et al.* 1963, 1964; Spradbery 1968, 1970; and Richerson and Borden 1972a, b). Habitat cues are even more important for some taxa, particularly when the parasite uses a

variety of hosts all found in the same habitat, shoots of conifers for instance (Townes 1960).

Some aculeate wasps that hunt concealed prey might also use habitat cues and/or token stimuli as the present study suggests.

## MATERIAL AND METHODS

*Euodynerus foraminatus* (Sauss.) was studied as part of a comparative work on prey-stinging methods (Steiner 1983).

Numerous field observations were made on this and other species of eumenine wasps in central Oregon, U.S.A., near Bend (Deschutes Co.) and Cove Palisades (Jefferson Co.) during the spring and summer of 1977. Marking of individual wasps was not very successful, presumably because the population under study was too large and the probability of sighting marked individuals repeatedly, very low. Consequently only general trends were studied, on a qualitative basis.

Individually marked wasps were then studied in cages about 50 x 80 x 50 cm (general methods described in Steiner 1965) and tested with various separate and combined stimuli. Unfortunately among the few that survived only one wasp (No. 1031), caught near Lower Bridge on June 2, came into reproductive condition and responded positively to the appropriate stimuli. No striking individual or species differences were recorded during the field observations. It is therefore felt that data gathered on this single individual are probably representative of the species. Previous studies of various wasps in captivity (from 1952 on) have also shown that prey-related activities are generally very stereotyped.

The stimuli used singly or in combination were: a) the prey itself, namely various unidentified leaf-rolling microlepidopteran larvae commonly found on trees or shrubs such as *Salix* spp., *Populus* sp., and also a few suitable leaf-rolling larvae of unidentified sawflies, also accepted by the wasp which is not very prey-specific; b) token stimuli produced by the prey, such as rolled leaves and/or the silk used to hold these leaves together, leaves rubbed on the prey or on frass (odor of prey); c) isolated leaves of various trees, shrubs or plants (mostly *Salix* spp.) taken from non-infested small shrubs or branches isolated from possible contacts by fine gauze wrapped around them. Complete absence of prey-related stimuli was confirmed later, on the basis of lack of any activating effects on the wasp (see results), whereas prey-related stimuli (silk, frass, etc.) invariably produced striking effects, described later, when the wasp was in hunting condition. To avoid contamination of the cage, stimuli were placed on pieces of aluminum foil removed after each trial. After stinging, the prey was also immediately removed from the cage before the wasp could carry them in the cage and disseminate the odor by contact.

In order to avoid or minimize conditioning of the wasp, patterning of the conditions of presentation was carefully avoided by varying widely and arbitrarily the time, order and location of presentation as well as the kind of stimulus situation. The stimuli were introduced in the cage very slowly, through a small lateral door in order to avoid sudden movement or mechanical disturbances that could have provided signals to the wasp. Leaves without prey or token stimuli and pieces of aluminum foil were also left routinely in the cage for extended periods of time in order to break any strong association of such objects with the reward of a prey (positive reinforcer).

## RESULTS AND DISCUSSION

**Field observations**

The major aim was to get some general idea about the methods of host-finding used by various eumenine wasps and females of *E. foraminatus* in particular. Such wasps were found in large numbers on various trees and shrubs, particularly *Salix* spp., *Populus* sp., *Alnus* sp., etc. along the banks of the Deschutes River. All eumenid wasps observed proceeded essentially in the same way. They inspected summarily (I in Table 1) a large number of individual leaves and after a while flew to another area of the same or a different tree. The pattern of searching changed drastically as they found rolled leaves, groups of leaves held together with silk (Fig. 1A), leaves covered with silk (Fig. 1B) or with frass. Such token stimuli were carefully investigated (SI in Table 1) with the antennae (Fig. 1B) and had clearly a special significance for the wasps. The latter became very agitated (activation = A in Table 1) and often started chewing vigorously the leaves or silk (CH in Table 1; Fig. 1A). The wasps intensified their search which also became much more localized. Their movements became very jerky and were oriented in many different directions. The wings were open and spread apart and the mandibles open, apparently in preparation for pouncing on a prey organism. If presence of a prey organism inside the rolled leaves was confirmed by antennal inspection, wasps then intensified their attack with the mandibles and chips of vegetation were detached from the base of the leaves (Fig. 1A) and the resulting hole was progressively enlarged. This hole and/or the open extremities of the rolled leaves were also frequently inspected and the wasps also poked their abdomen tip into them, in an apparent effort to deliver one or several sting(s), haphazardly, to the invisible prey (= irregular stings: Steiner 1983). Some prey organisms dropped to the ground very suddenly or remained suspended at the end of a thread of silk. Presented with this circumstance, many wasps remained on the vacated leaves, apparently activated by the still present odor of the prey. At other times the wasps were successful in extracting the prey and immediately undertook to sting them into paralysis with one, two or more stings in the cephalo-thoracic region (details in Steiner 1983: regular stings; see also Fig. 1C). *E. foraminatus* females exhibit little prey-specificity but take only rather small, frail caterpillars such as those of Gelechiidae, Oecophoridae, Olethreutidae, Tortricidae, Pyraustinae, Pyralidinae, etc. (Krombein *et al.* 1979, p. 1495). A few leaf-rolling larvae of sawflies were also accepted. The same lack of strict specificity also appears to hold for the vegetation visited by such wasps.

**Study in captivity**

Control of variables of the stimulus situation, however imperfect, is possible only under laboratory conditions. In particular, presence of prey-odor on the leaves investigated in the wild could not be ruled out. The results of 53 trials with various stimulus situations are summarized in Table 1. Interpretation of the results requires some preliminary comments. First, such experiments should involve independent samples, but the number of wasps required would have been prohibitive because they are difficult to raise, and in fact only one wasp survived. Second, the measured durations (cols. 3 and 4) are highly variable or were not determined (priority was given to stinging patterns). Therefore, for these various reasons, a statistical analysis would not be meaningful. Furthermore, probability of detection of the stimuli presented does not remain constant over time since it depends among other things on: 1) the internal state of the wasp, which fluctuates over time, both on a short- and long- term basis; 2) location of the wasp relative to that of the stimulus situation presented also varied considerably; 3) the general level

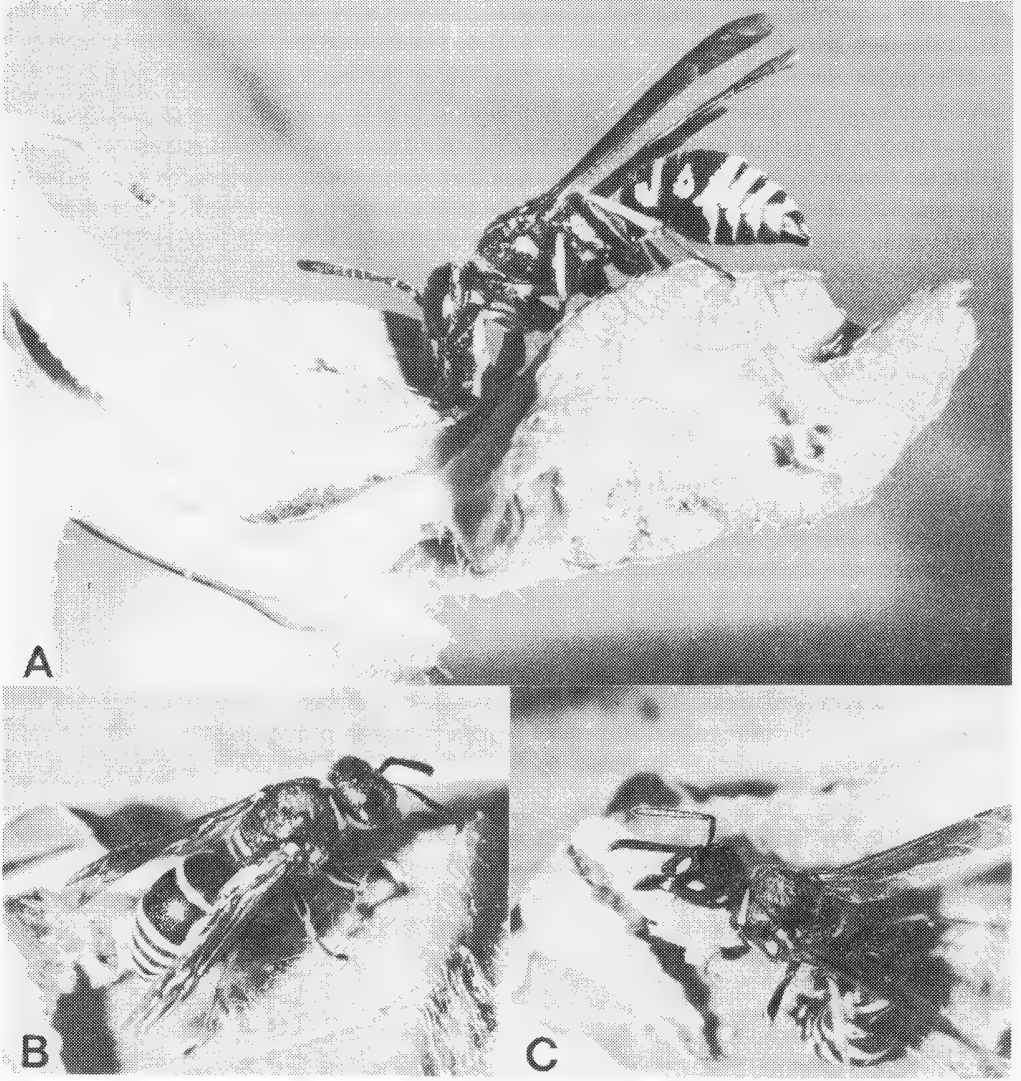


Fig. 1. *Euodynerus foraminatus* wasp carefully investigating (A) a group of leaves held together by silk threads spun by a larva of Microlepidoptera or Tenthredinidae; the wasp starts attacking the base of the shelter with her mandibles; (B) silk threads covering a *Salix* leaf are probed with the antennae and then chewed with the mandibles; (C) after extraction of the caterpillar from its shelter, the wasp stings the prey into paralysis.

Table 1. Results of 53 trials (tests) with various stimulus situations presented to wasp No 1031 (*Euodynerus foraminatus*) in captivity. List of abbreviations: *col.2*: L=leaves (in parenthesis: S=*Salix* spp., P=*Populus* sp., V=*Verbascum [thapsus?]*, P=*Plantago* sp., L=lettuce, G=green grasshopper, ?=non-identified); P=prey (various suitable larvae of microlepidopterans, mostly leaf-rollers; a few tenthredinid larvae); T=token stimuli (in parenthesis: R=rolled leaves, S=silk threads on leaf, O=odor on leaf) - *Cols 3 & 4*: m=minutes; s=seconds (if preceded by f, means a few minutes or seconds); X: visit of undetermined duration, preceded by number indicating number of visits; successive visits separated by commas - *Col.5*: I=short investigation; SI=sustained (careful) inspection; A=activation effects ("arousal"); CH=chewing excitedly the vegetation and/or token stimuli; ST=stinging of prey (number in parenthesis refers to diagram showing stinging pattern in Fig. 3 of Steiner, 1983).

1 Presentation time			2 Stimulus situation	3 Latency of discovery	4 Duration of interaction(s)	5 Effect(s) on wasp
Month	Day	Hour				
Jn	19	1310	L(?) + T(R) + P	fs	m:7,5	SI, A, CH
		1324	id	fs	m:3, 1-2?, 1-2?, X, 13, 3X	SI, A, CH
		1440	id	fs	X, 2X	I
		1515	P	fs	m:10	SI, A, ST
		1321	P	not found	/	/
	20	1325	P	id	/	/
		1331	P	id	/	/
		1400	L(V)	m:64	X (short)	I
	30	1545	id	m:19	id	I
		1105	L(S) + P	not found	/	/
Jl	5	?	L(S) + T(S)	?	m:20+, 2X	SI, A, CH
		1515	L(S) + T(S+O)	fs	?	SI, A
		1528	L(S) + T(S) + P	fs	?	SI, A, ST(1)
		1110	L(S) + P	m:50	fs	I(pre not found)
		?	L(S) + P	?	fm	SI, A, ST(2)
	7	1140	L(S) + P	m:3	fm	I(pre not found)
		?	L(S) + P	?	fm	SI, A, ST(3)
	10	1121	L(S) + P	m:9	fm	SI, A, ST(4)
		1220	id	fs	fm	SI, A, ST(9)
		1242	id	m:15	fm	SI, A, ST(13)
		?	L(S)	?	fs, X (short)	I, I

(continued on next page)

Table 1 (continued)

1 Presentation time MonthDay . Hour		2 Stimulus situation	3 Latency of discovery	4 Duration of interaction(s)	5 Effect(s) on wasp
11	1352	L(P) + P	m:8	fm	SI, A, ST(18)
	1200	L(S) + T(S)	fs	X, X, X...? (short)	I, SI, A, CH
	1207	L(S) + T(S) + P	m:3	fm	I, SI, A, ST(10)
	?	L(S)	?	X, X... (short)	I, I...
	1245	L(S) + P	m:3	2X, X (short)	I, I, I
	1300	id	m:5	fm	SI, A, ST(14)
	?	L(S) + T(S)	?	2X	SI, A, CH, I
	?	L(S) + P	?	?	SI, A, ST(19)
	1423	P	m:2	fm	SI, A, ST(5)
	?	L(L)	?	fs	I
12	1328	P	m:2	m:10	SI, A, ST(20)
	1340	L(P)	not found	/	/
	1608	P	m:20	fm	SI, A, ST(15)
	1656	P	m:3	fm	SI, A, ST(11)
	1707	P	m:8	fm	SI, A, ST(6)
	1800	L(S)	fs	fs	I
	1803	L(S) + P	m:4	m:3	SI, A, ST(12)
13	1815	id	m:3	fm	SI, A, ST(7)
	1825	id	m:3	fm	SI, A, ST(16)
	1836	id	m:1	fm	SI, A, ST(21)
	1330	L(S)	fs	X (very short)	I
	1333	L(S) + P	fs	fm	SI, A, ST(8)
	?	L(S)	?	X (very short)	I
	?	L(S)	?	id	I
14	1540	L(S) + P	fs	fm	SI, A, ST(17)
	?	L(S)	?	X (very short)	I
	1040	L(V)	?	X, X, X... (short)	I, I, I...
	1616	G	?	X, X... (short)	I, I...
	1130	L(S) + T(S) + P	fs	fm	SI, A, CH, ST(22)
29	1543	L(S) + P	m:4	fm	SI, A, ST(23)
30	1158	L(S)	fs	X(short)	I
	1210	L(S) + P	?	fm	SI, A, ST

of exploratory activity of the wasp was also very variable and could not be controlled or quantified. Effects on the wasp (col. 5) were very clear cut, however, which will therefore be

emphasized.

Results of the tests suggest the following. 1) Most latencies of discovery (col. 3) were short or even very short (a few minutes or seconds); this indicates that the wasp under hunting conditions was very attentive to presence and absence of relevant stimuli in the environment. 2) Leaves devoid of prey or prey-related stimuli (L situation in col. 2) were readily discovered and investigated, but only summarily (I in col. 5) and they did not produce detectable activating effects on the wasp (A in col. 5). Therefore, detection and investigation do not depend on presence of token stimuli and vegetation represents only a habitat cue, presumably detected on the basis of color (green). Incidental observations also point to the probable importance of color: first, on July 19 the wasp investigated a rather large green acridine (slanted-faced) grasshopper, among many brownish oedipodine grasshoppers, that were ignored (grasshoppers were given as prey to *Prionyx parkeri* wasps, also present in the same cage); second, the wasp once escaped from the cage into the field trailer used as "mobile laboratory" and after flying in various directions finally landed on the only green object, an old dried up leaf of *Salix*, discarded from previous trials. In natural conditions, shape of plants, shrubs and trees probably provides additional cues, detected at greater distances. Reactions to color should be systematically investigated, however, and dissociated from shape and vegetation. 3) The low specificity of the vegetation investigated, noticed in the wild, is fully confirmed by tests which included even leaves of lettuce, a plant not associated with suitable prey or token stimuli. Therefore cues such as green vegetation and/or other habitat cues contribute to focus the search of these wasps. 4) In sharp contrast, "token" stimuli (T, col 2) such as rolled leaves [ (R), col. 2], odor left on leaves [ (O), col. 2], and silk [ (S), col. 2] had much more specific, selective, effects (situations L+T, L+T+P, col. 2). They were extensively inspected with the antennae (SI, col. 5) and produced clear activating effects (A, col. 5) on the wasp, including chewing (CH, col. 5) that was not observed with leaves devoid of prey-related stimuli. 5) Only the prey itself, a still more specific stimulus, elicited stinging (ST, col. 5) (cutworm-hunting *Podalonia luctosa* sphecids wasps, tested with single small leaves of dandelion rubbed with cutworm frass, occasionally attempted to sting such leaves, after having assumed the appropriate stinging posture). 6) Only certain areas of the body of the prey receive regular stings (details in Steiner 1983); therefore these various stimuli are organized into a hierarchy involved in increasingly selective responses of the wasp, namely: habitat cues < token stimuli < suitable prey < suitable stinging sites on prey.

Finally, the question of whether habitat cues (vegetation) and/or token stimuli (silk, frass, rolled leaves, odor left on vegetation) are recognized innately or on the basis of their association with the prey (by imprinting or by conditioning) remains open. To solve this problem one would have to use naive wasps that had never been in contact with a prey before. Conditioning was discouraged, however, by withholding the reward of a prey (=positive reinforcer) for extensive periods of time in the cage ("unlearning").

## CONCLUSION

Eumenine wasps that hunt hidden prey such as larvae of leaf-rolling Microlepidoptera have evolved a host-finding strategy which is very similar to that used by some parasitic wasps such as wood wasps (Siricidae). It is based on the use of habitat cues and/or token stimuli left behind by the prey. Predictability and reliability of prey-habitat associations appear crucial however. Thus females of the sphecids wasp species *Prionyx parkeri*, studied in the wild in

southeastern Arizona, hunt euryphagous oedipodine grasshoppers which are highly mobile and exposed, and not restricted to any special microhabitat. Consequently the hunting wasps run haphazardly over the ground until they find a prey specimen, without appearing to use any habitat cue or token stimuli to focus their search (Steiner 1981a, b). On the other hand such prey are usually very abundant and the probability of chance encounters very high. In contrast *Podalonia valida* wasps, studied in the same habitat, hunt predominantly or exclusively the much less common lepidopterous larvae of the arctiid ("woolly bears") and systematically inspect plants such as horsemint (*Monarda pectinata*), goldweed (*Verbesina encelioides*) and various "sunflower-like" plants where such prey were usually found (Steiner 1974, 1975). *Prionyx* wasps also visit such plants but only for feeding, resting or sleeping, not during hunting. Previous studies in captivity of numerous sphecids and other eumenine wasps (from 1952 on) have shown that some other wasps such as caterpillar hunters (*Podalonia luctosa*, *Ammophila azteca*, etc.), aphid hunters (*Pemphredon* spp.), various gorytine wasps that hunt leaf hoppers (also *Mimesa* sp.), and curculionid hunters such as *Cerceris* spp. also pay much attention to any vegetation introduced in the cage, while they are hunting. Detailed comparisons among species will be presented elsewhere, along with information on other wasps that hunt hidden prey or prey with restricted habitats or feeding habits.

In summary it is clear that host-finding based on habitat cues and/or token stimuli left behind by the prey is found mostly or exclusively in species that hunt hidden prey or prey species that live in very selective, predictable, habitats. This strategy evolved independently and convergently in wasps as diverse as Ichneumonidae, Siricidae, Braconidae, Eumenidae and Sphecidae.

#### ACKNOWLEDGEMENTS

The wasp material was kindly identified by R.M. Bohart, Department of Entomology, University of California, Davis, U.S.A. I would like to thank R. Longair for long discussions on the present topic. Research was supported by a grant from the NRCC (No A3499) and funds from the University of Alberta.

#### REFERENCES

- Heatwole, H., D.M. Davis and A.M. Wenner. 1963. The behaviour of *Megarhyssa*, a genus of parasitic hymenopterans (Ichneumonidae: Ephialtinae). *Zeitschrift für Tierpsychologie* 19: 652-664.
- Heatwole, H., D.M. Davis and A.M. Wenner. 1964. Detection of mates and hosts by parasitic insects of the genus *Megarhyssa* (Hym.: Ichneumonidae). *American Midland Naturalist* 71: 374-381.
- Krombein, K.V., P.D. Hurd Jr., D.R. Smith and B.D. Burks. 1979. Catalog of Hymenoptera in America North of Mexico. Vol. 2: Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C.
- Richerson, J.V. and J.H. Borden. 1972a. Host finding behaviour of *Coeloides brunneri* (Hym.: Braconidae). *Canadian Entomologist* 104: 1235-1250.
- Richerson, J.V. and J.H. Borden. 1972b. Host finding by heat perception in *Coeloides brunneri* (Hym.: Braconidae). *Canadian Entomologist* 104: 1877-1881.
- Spradbery, J.P. 1968. The biology of *Pseudorhyssa sternata* Merrill (Hym., Ichneumonidae), a



- cleptoparasite of siricid woodwasps. *Bulletin of Entomological Research* 59: 291-297.
- Spradbery, J.P. 1970. Host finding by *Rhyssa persuasoria* (L.) an ichneumonid parasite of siricid woodwasps. *Animal Behaviour* 18: 103-114.
- Steiner, A.L. 1965. Mise au point d'une technique d'élevage d'Hyménoptères fouisseurs en laboratoire (Note préliminaire). *Bulletin de la Société entomologique de France* 70: 12-18.
- Steiner, A.L. 1974. Unusual caterpillar-prey records and hunting behavior for a *Podalonia* digger wasp: *Podalonia valida* (Cresson) (Hym.: Sphecidae). *Pan-Pacific Entomologist* 50: 73-77.
- Steiner, A.L. 1975. Description of the territorial behavior of *Podalonia valida* (Hym., Sphecidae) females in southeast Arizona, with remarks on digger wasp territorial behavior. *Quaestiones Entomologicae* 11: 113-127.
- Steiner, A.L. 1981a. Anti-predator strategies. II. Grasshoppers (Orth., Acrididae) attacked by *Prionyx parkeri* and some *Tachysphex* wasps (Hym., Sphecinae and Larrinae): a descriptive study. *Psyche* 88: 1-24.
- Steiner, A.L. 1981b. Digger wasp predatory behavior (Hym., Sphecidae). IV. Comparative study of some distantly related Orthoptera-hunting wasps (Sphecinae vs Larrinae), with emphasis on *Prionyx parkeri* (Sphecini). *Zeitschrift für Tierpsychologie* 57: 305-339.
- Steiner, A.L. 1983. Predatory behaviour of solitary wasps. V. Stinging of caterpillars by *Euodynerus foraminatus* (Hym.: Eumenidae): weakening of the complete four-sting pattern. *Biology of Behaviour* 8: 11-26.
- Townes, H.K. 1960. Host selection patterns in some Nearctic ichneumonids (Hym.). *Proceedings of the XIth International Congress of Entomology* 2: 738-741.



TYPE LOCALITY RESTRICTIONS AND LECTOTYPE DESIGNATIONS FOR THE  
"ROCKY MOUNTAIN" BUTTERFLIES DESCRIBED BY EDWARD DOUBLEDAY IN  
"THE GENERA OF DIURNAL LEPIDOPTERA" 1847-1849

Jon H. Shepard  
R.R. #2, Sproule Creek Road  
Nelson, British Columbia  
V1L 5P5

*Quaestiones Entomologicae*  
20: 35-44 1984

ABSTRACT

*Doubleday described six species of butterflies from the Rocky Mountains of North America in his "Genera of Diurnal Lepidoptera", Parnassius smintheus, Anthocharis creusa, Argynnis astarte, Melitaea anicia, Erebia mancinus, and Chionobas chryxus. The type locality of the six has been erroneously cited as near Banff, Alberta by authors. Evidence is presented to show that the type material was collected near Jasper, Alberta. Except for Argynnis astarte, each species is represented by two syntypes in the British Museum collection. Appropriate lectotypes have been designated.*

RÉSUMÉ

*Dans son ouvrage intitulé "Genera of Diurnal Lepidoptera", Doubleday décrit six espèces de papillons provenant des Montagnes Rocheuses nord-américaines; ces espèces sont Parnassius smintheus, Anthocharis creusa, Argynnis astarte, Melitaea anicia, Erebia mancinus, et Chionobas chryxus. Certains auteurs citèrent par erreur la localité typique de ces espèces comme étant près de Banff en Alberta. Le présent auteur avance des preuves démontrant que le matériel typique fut collectionné près de Jasper en Alberta. À l'exception d'Argynnis astarte, chaque espèce est représentée par deux syntypes dans la collection du British Museum, pour lesquels l'auteur désigne des lectotypes.*

INTRODUCTION

Edward Doubleday described six species of butterflies from the "Rocky Mountains" of North America: *Parnassius smintheus* 1847, *Anthocharis creusa* 1847, *Argynnis astarte* 1847, *Melitaea anicia* 1847, *Erebia mancinus* 1849, and *Chionobas chryxus* 1849. The modern combinations of these names are, respectively: *Parnassius phoebus smintheus*, *Euchloe creusa*, *Clossiana astarte*, *Occidryas anicia*, *Erebia disa mancinus*, and *Oeneis chryxus*. The type locality for all six species was given as Rocky Mountains. The description of *P. p. smintheus* contains the additional information that it was collected in the summer of 1845 by Lord Derby's collector, Mr. Burke. An error was made in the addenda and corrections, p. 531, giving the type locality of *C. astarte* as Jamaica (Westwood, 1852).

The contradiction of Jamaica and Rocky Mountains threw into confusion the actual type locality of all six species. Between 1851 and 1891 most effort was concentrated on locating the source of *C. astarte* (Fletcher, 1908). Opinion as to the actual source of *C. astarte* was divided between the majority who thought it occurred in the mountains of British Columbia (Elwes, 1889; Strecker, 1882) and the minority represented by William H. Edwards who believed *C. astarte* to be a subspecies of *Speyeria mormonia* (Bdv.) from California (Brown, 1965). When Thomas Bean sent specimens of *C. astarte* to W.H. Edwards these were first described as

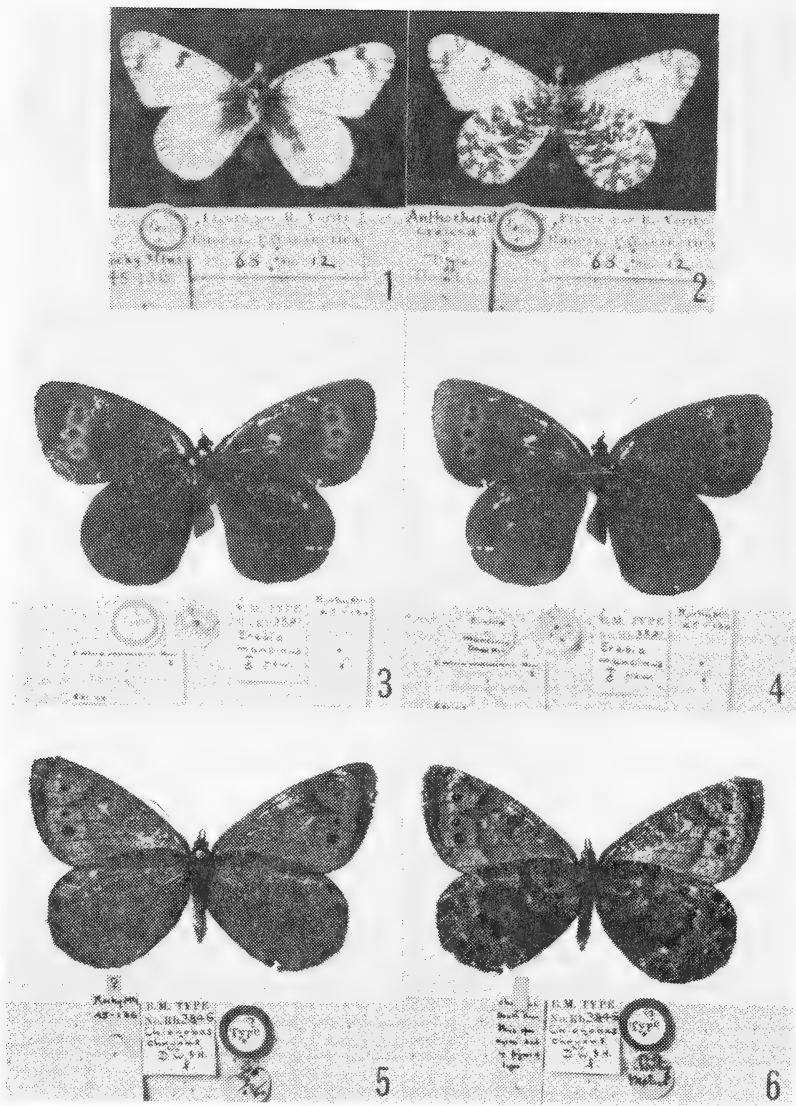


Fig. 1. Lectotype of *Anthocharis creusa*, upperside. Fig. 2. Lectotype of *Anthocharis creusa*, underside. Fig. 3. Lectotype of *Erebia mancinus*, upperside. Fig. 4. Lectotype of *Erebia mancinus*, underside. Fig. 5. Lectotype of *Chionobas chryxus*, upperside. Fig. 6. Lectotype of *Chionobas chryxus*, underside.

*Argynnis victoria* (Edwards, 1891), type locality Laggan, Alberta. Laggan is now known as Lake Louise, Alberta. Since this second collection of *C. astarte*, the type locality of all six species has been attributed to the vicinity of Banff, on the mistaken assumption that Banff was frequented by white men at the time *C. astarte* was collected.

F.M. Brown's statement to Opler (1967) is representative of established opinion concerning the type locality of Doubleday's species names: "the great majority of North American specimens collected by Lord Derby came from the vicinity of Banff, Alberta. I doubt that he got over to the B.C. side of the range and it is questionable that he got as far north as "Kicking Horse Pass". Brown's statement contained another major confusion. Lord Derby, who presented the material to the British Museum of Natural History, did not collect the specimens. He either sent out professional collectors, such as Mr. Burke, or he obtained specimens from persons who had returned to England from world travels. Lord Derby, the thirteenth Earl, never travelled to western North America. In 1848 the future fifteenth Earl travelled to eastern Canada and the United States returning to England via the West Indies. The published diaries of the fifteenth Lord Derby's travels combined with the typographical error of recording *C. astarte* from Jamaica may account for the confusion of earlier authors.

For two of the species involved, *Euchloe creusa* and *Clossiana astarte*, authors have attempted to restrict the type localities to specific points. Opler (1967) restricted the type locality of *E. creusa* to the vicinity of Banff, Alberta. Pike (1980) restricted the type locality of *C. astarte* to Mount Cheam, British Columbia. Both authors were incorrect.

In crediting all the names to Doubleday and not to Hewitson or Westwood or some combination of the three names, the interpretation of Hemming (1941) is followed; that of Miller and Brown (1981) is ignored. Hewitson only drew the plates and was not responsible for the names attached. Thus, Doubleday is the sole author of the names.

Miller and Brown (1981) made the following errors in referring to the species discussed in this paper. For the species *O. anicia*, *E. disa mancinus* and *O. chryxus* they stated that each holotype is in the British Museum. There are only syntypes for these three species. The original description of *P. p. smintheus* first appeared on page 26, a fact also overlooked by Hemming (1941). The first place where the name *E. creusa* appeared in print was pl. 7, fig. 1 Hemming, 1941), not p. 56. The date of publication of the name *O. anicia* was 1847 (Hemming, 1941), not 1848. The name *Erebia disa mancinus* first appeared on pl. 64, fig. 2, not pl. 63, fig. 2. Also the name *E. d. mancinus* was first published in 1849 on the same plate as the name *O. chryxus*, and not in 1851. The name *chryxus* was first published on 2: pl. 64, fig. 1, not 1: pl. 64, fig. 2.

## DISCUSSION OF TYPE LOCALITY

The original descriptions of the six species state that each was from the Rocky Mountains. In addition, it is stated that the specimens of *Parnassius phoebus smintheus* were collected in the summer of 1845 by Lord Derby's collector, Joseph Burke. There is no indication in the text that all six species were, or were not, collected by one collector or at one locality. Examination of the various series in the British Museum of Natural History shows that all specimens were presented to the Museum in either 1845 or 1847 by Lord Derby with at least one specimen of each of the six species donated in 1845 (see Table 1.). The locality information given on labels is "Rocky Mountains" with no indication of the collector. Two possible clues to the original source of the specimens are the extant correspondence of Lord Derby and information concerning Joseph Burke.

Table 1. Summary of dates of publication and type specimens in the British Museum of Natural History.

NAME	DATE OF PUBLICATION (HEMMING, 1941)	SPECIMENS DONATED TO BMNH	
		1845	1847
<i>Parnassius (phoebus) smintheus</i>	1847	1♂	1♂
<i>Anthocharis (Euchloe) creusa</i>	1847	2♂	—
<i>Argynnis (Clossiana) astarte</i>	1847	1♀	—
<i>Melitea (Occidryas) anicia</i>	1847	1♀	1♂
<i>Erebia (disa) mancinus</i>	1849	1♂	1♂
<i>Chionobas (Oeneis) chryxus</i>	1849	2♀	—

The standard publications about British botanists and Rocky Mountain naturalists (Britten & Boulger, 1931; Ewan, 1950) gave Joseph Burke's itinerary in North America as between Fort Hall, Idaho and the upper reaches of the Platte River between 1844 and 1846. This is further substantiated by Allen (1848) who states that she encountered Mr. Burke just east of Soda Springs, Idaho on September 27, 1945. Thus, it seems possible that the type locality of *P. smintheus*, which Doubleday stated was collected in 1845, could be placed in southeastern Idaho or Wyoming. However, only two of the five remaining species, *Oeneis chryxus* and *Occidryas anicia* could have been collected in this area. *Euchloe creusa* occurs only as far south as Waterton Lakes Park, Alberta (Opler, 1970). *Clossiana astarte* occurs only as far south as Glacier National Park, Montana (Kohler, 1980). *Erebia disa mancinus* occurs only as far south as Canmore, Alberta (Bird & Kondla, pers. corr.). Examination of the type specimens of the three species which could have been collected between Fort Hall, Idaho and Platte River, Wyoming is of no help in deciding where they were collected, as phenotypic variation of individuals of any one population of any of these three species is notorious.

Regarding *Erebia disa mancinus*, *Euchloe creusa* and *Clossiana astarte*, one must assume that at least the type specimens of these three species were collected at one locality. To assume otherwise would imply that Lord Derby received butterfly specimens from a variety of localities and collectors when in fact, he normally did not receive any butterflies, only plants, birds and mammals. That one locality must be somewhere in the Canadian Rockies. *Euchloe creusa* and *Erebia disa* do not occur in the areas of Washington State and the Coast Range of British Columbia where disjunct populations of *Clossiana astarte* occur. The area of the Rocky Mountains where all three are known to occur extends from Pink Mt., British Columbia in the north to Canmore, Alberta in the south.

In the summer of 1845 and previously there was only one area of this region of the Rocky Mountains which was accessible to white men. The Hudson's Bay route connecting Fort Vancouver and other posts west of the Rocky Mountains with York Factory, Manitoba went from Jasper House, Alberta over Athabasca Pass to Boat Encampment, Columbia River, British Columbia. This was the only area where *Clossiana astarte* could have been collected. *Clossiana astarte* occurs only above timberline. Nowhere else did the Hudson's Bay route go near timberline. It may seem dogmatic to make such a statement. However, one must appreciate the control the Hudson's Bay Company had on the territory of its mandate. After

1821 when the Hudson's Bay Company, based in London, and the Northwest Company, based in Montreal, were merged the Hudson's Bay Company had complete control over the area. No one was allowed to travel through without the express permission of the company. Since the Hudson's Bay Company directed all supplies and travel routes they could enforce this control.

There are several possible sources of Lord Derby's Rocky Mountain material. The first non-Hudson's Bay employee to be in the vicinity of Jasper and Athabasca Pass was the naturalist Thomas Drummond (Soper, 1970; MacGregor, 1978). Drummond collected insects in the vicinity of Jasper in 1826 and 1827. These were described by Kirby (1837). None of these were butterflies, even though Kirby did describe butterflies collected by Drummond further east in Canada. Examination of Lord Derby's correspondence revealed no letters written to or received from Mr. Drummond (I.D. Wallace, pers. corr.). Thus, it does not seem likely he was the source of Lord Derby's specimens. David Douglas, the botanist, also passed through Athabasca Pass in 1827. Since his journals (Douglas, 1914) show he never collected insects, he could not have been the source of Lord Derby's specimens. Soper (1970) recorded still a third naturalist as going over Athabasca Pass in 1827 in company with Douglas. This was Edward Ermatinger. Ermatinger's journals (Ermatinger & White, 1913) show that he travelled over the pass May 1, 1827, October 8, 1827 and May 2, 1828. These dates are not remotely within the flight period of *C. astarte* and thus Ermatinger could not have been the source of *C. astarte*. These dates represent the dates that the Spring and Fall mail and furs always went over the pass (Judith Beattie and the author's examination of Hudson's Bay Archives, Winnipeg, Manitoba). Thus, a casual day's collecting by a Hudson's Bay employee while traveling with the cargo could not have been the source of Lord Derby's specimens. Only a factor at Jasper House or a non-Hudson's Bay employee, resident in the general area for a summer between the Spring and Fall movement of cargo, could have collected *C. astarte* and other butterflies. There is no evidence that any Factor at Jasper House collected natural history specimens or corresponded with Lord Derby. Soper (1970) indicated that the next non-Hudson's Bay Employee to reach Jasper area for a summer's residence was the artist Paul Kane in 1846. This is after Lord Derby donated the specimen of *C. astarte* to the British Museum.

The evidence suggests that the butterflies described by Doubleday were not collected near Jasper, even though this was the only possible place they could have been collected. However, in reaching this conclusion, the itinerary of Joseph Burke, the stated collector of *P. p. smintheus*, has been either ignored or stated incorrectly. Drury (1940), Macleod (1947), MacKelvey (1955) and Glover (1975) give accurate facts about Mr. Burke's itinerary. Letitia Hargrave's letters (Macleod, 1947) record meeting Mr. Burke in the Fall of 1843 at York Factory when he was preparing to leave for Edmonton House. Drury (1940) quoting a letter from the botanist C.A. Geyer to Sir William J. Hooker, states that Geyer encountered Mr. Burke at Fort Walla Walla in the Fall of 1844 after Mr. Burke had spent the previous summer at "Jasper's House". MacKelvey (1955) gives the first relatively full and accurate account of Joseph Burke's travels in North America based on sixteen letters written by Burke to Sir William Hooker. In these letters Burke stated that he spent the entire summer of 1844 near Jasper House using the same Indian guide and camping at the same spot as Thomas Drummond did in 1827 (MacKelvey, 1955). The long stay near Jasper was not in Burke's original plans. A heavy snow the previous winter prevented the usual Spring trip over Athabasca Pass. Also the weather during the summer of 1844 was very poor. Burke apparently collected butterflies to augment his otherwise poor collecting season. In a letter to Lord Derby sent from Jasper House dated 10 September

1844, Burke stated that he was sending "a small box of butterflies" (Glover, 1975). On 17 October 1846, Burke wrote to Hooker stating he was unable to ship any specimens to Hooker or Derby between 10 September 1844 and February 1846 when Burke arrived at Fort Vancouver (MacKelvey, 1955). There is no evidence to suggest that material sent in February 1846 or later contained butterflies. Only plant specimens were mentioned. Thus, Doubleday is presumably incorrect in stating *P. p. smintheus* material was collected in 1845. These specimens must have been collected in 1844. Since it is known that Burke sent Lord Derby a small package of butterflies from Jasper House, and there is no evidence that anyone else sent Lord Derby any butterflies from North America, I assume that specimens of all six species of Rocky Mountain butterflies presented to the British Museum of Natural History were collected by Burke near Jasper, Alberta.

Bird (1967) gives a detailed account of Thomas Drummond's itinerary in the Rocky Mountains pinpointing the site near Jasper which both Drummond and Burke (MacKelvey, 1955) used as a summer base camp. This site is "Stony Lake" (now Rock Lake: 53° 27'N, 118° 16'W), Alberta. This area in the vicinity of Rock Lake is the type locality of the Doubleday names.

Opler (1967) restricted the type locality of *Euchloe creusa* to the vicinity of Banff, Alberta on the recommendation of F.M. Brown. This has been shown to be incorrect. Pike (1980) restricted the type locality of *Clossiana astarte* to Mount Cheam, British Columbia, based on the fact that Laggan was unexplored and that "it seems resonable to restrict the type locality of *B. astarte* to the locality nearest the major cities of British Columbia around 1800-1820". Pike assumed that British Columbia was well explored at the time *C. astarte* was collected, but this is not correct. Between 1800 and 1820 the only settlement on the west coast of British North America was Nootka Sound on the west coast of Vancouver Island (Ormsby, 1971). The next British settlement was Fort Vancouver on the Columbia River, established March 19, 1825 (Ormsby, 1971). There were no villages, let alone major cities. Both Victoria and Vancouver, British Columbia were established after Lord Derby's specimens were collected.

Even disregarding Pike's error about British Columbia settlements and assuming that specimens of *Clossiana astarte* may have reached Lord Derby via a second collector, a highly unlikely event as none of Lord Derby's voluminous and well preserved correspondence indicates such, Mount Cheam is not a possible locality where *C. astarte* could have been collected previous to 1846. From 1821 when the Hudson's Bay Company took over the Northwest Company, the major travel route was west from York Factory, Hudson Bay through Edmonton, Jasper House, Athabasca Pass, Boat Encampment on the Columbia River and then down the Columbia past Ford Colville to Fort Vancouver. Two attempts to follow the Fraser River west past Mount Cheam were unsuccessful and the route was abandoned. No natural history specimens were collected during these two attempts. Possible access to Mount Cheam via the west would have had to pass through Fort Langley, British Columbia. Fort Langley was established in the Spring of 1828 by George Barnston. Barnston's Fort Langley journals do not mention collecting or travels to any nearby mountains (Judith Beattie, pers. corr.). That October, A. McDonald was put in charge of Fort Langley where he remained until the summer of 1833. McDonald's biography (Cole, 1979) indicates that the only contact with the outside world was the yearly boat from Fort Vancouver. No mention is made of any traveling naturalist. Such an event would have been the highlight of any year when the annual boat from Fort Vancouver was the only contact with other Europeans. Further, there is no known correspondence between McDonald and Lord Derby. In 1833, McDonald was transferred to



Fort Colville where he remained until September 21, 1844. During the entire period, 1828-1844, McDonald carried on an extensive correspondence with other Hudson's Bay Company employees and was aware of all the events happening in British Columbia (Cole, 1979). In a letter to Hooker (Cole, 1979), McDonald states "I am extremely sorry to have to report that, with the single exception of our mutual friend Mr. Tolmie, the Gents, of the west side (B.C. & Wash.) are very reluctant to dab in anything connected with the vegetable or animal kingdom". The said Mr. Tolmie was based at Nisqually, Washington, far removed from the known range of *C. astarte*. After McDonald left, Fort Langley remained an outpost accessible only via boat from the west until 1848 (Ormsby, 1971). In the summer of 1848 the first successful attempt to cross the Cascades to Yale was completed. This change of route was forced on the Hudson's Bay Company by the loss of their routes on the Columbia River in the United States. The Yale route proved unusable and in 1849 Fort Hope was established as the western portal of the Coquihalla River Route from the east. Thus, there was no access to Mount Cheam until after *C. astarte* was collected. Pike (1980) was, therefore, incorrect in restricting the type locality of *C. astarte* to Mount Cheam.

In light of the evidence presented above, the type locality of *Parnassius smintheus*, *Anthocharis creusa*, *Argynnis astarte*, *Melitaea anicia*, *Erebia mancinus*, and *Chionobas chryxus* is formally restricted to the vicinity of Rock Lake, Alberta (53° 27'N, 118° 16'W).

#### LECTOTYPE DESIGNATIONS

The specimens on which Doubleday based his descriptions of the six species discussed above are all in the collection of the British Museum of Natural History. Five of the six species described are each represented in the British Museum of Natural History collection by two syntypes (see Table 1.). Doubleday did not label type specimens and thus lectotypes need to be selected. The sixth species, *Clossiana astarte*, is represented by a single female specimen which must be regarded as the holotype. The type specimen will be illustrated in a forthcoming paper on *C. astarte*. Since the discussion restricting the type locality requires the specimens be collected in 1844, I am using specimens presented by Lord Derby in 1845 as lectotypes. This is critical for *Parnassius phoebus smintheus* and *Occidryas anicia* where the specimens presented by Lord Derby in 1847 might later prove to have been collected between Fort Hall and the upper reaches of the Platte River instead of near Rock Lake, Alberta. This would radically alter historic usage of the names. For *Erebia disa mancinus* it would not be critical as this species could not have been collected in Wyoming or Idaho. However, the 1845 specimen has been isolated in the type collection and regarded as the type.

The lectotype of *Parnassius smintheus* Doubleday is the male specimen presented to the British Museum of Natural History in 1845 and labeled: Syntype, Rocky Mts. Pres. by Earl of Derby, 45-136, 33.6, spec. exam C. Eisner. The following label is being attached: Lectotype of *Parnassius smintheus*, designated by Jon H. Shepard, 1983. The male specimen labeled 47-74, Rocky Mts. Pres. by Earl of Derby, Type H.T. and photographed by C.F. dos Passos, B.M. photo #17177-17178, is not considered for lectotype or paralectotype designation. Nowhere in the literature has it been chosen as a lectotype, holotype, or in any way specified as the type specimen. The specimen designated as lectotype will be illustrated in a forthcoming paper on the type material of North American *Parnassius*. Barnes and McDunnough (1916) quote a letter from Sir George Hampson stating that the type series contained three males and one female. If this were true then one male and one female have been lost in the intervening years.

It is more likely that either Hampson or Barnes and McDunnough made an error, especially since on a following page Barnes and McDunnough misquote the figure numbers from Verity for illustrations of *Euchloe creusa*, another species of the same Doubleday material.

The lectotype of *Anthocharis creusa* Doubleday is the male specimen presented to the British Museum of Natural History in 1845 and labeled: Type, Rocky Mtns., 45-136, Figure par R. Verity, Rhopal. Palaearctica, pl. 68, fig. 12. The following label is being attached: Lectotype of *Anthocharis creusa* Doubleday, designated by Jon H. Shepard, 1983. This specimen was photographed by C. F. dos Passos and is illustrated here (figs. 1, 2). The second male specimen, labeled: Rocky Mtns. 45-136, is designated a paralectotype and labeled such.

The lectotype of *Melitaea anicia* Doubleday is the female specimen presented to the British Museum of Natural History in 1845 and labeled: Rocky Mtns., Pres. by Earl of Derby, 45-136. The following label is being attached: Lectotype of *Melitaea anicia* Doubleday, designated by Jon H. Shepard, 1983. This female specimen is the one that most closely matches the figure in the original description. It was again illustrated by Gunder (1929). Gunder also illustrated the male specimen presented by Lord Derby in 1847 and labeled it "type ♂ anicia". This did not represent an official lectotype designation and is herein disregarded. This specimen is not considered a paralectotype.

The lectotype of *Erebia mancinus* Doubleday is the male specimen presented in 1845 and labeled: Rocky Mtns., 45-136, B.M. type no. Rh. 3581, *Erebia mancinus* ♂ Hew., agrees with the figure of type. F.A.H., 8-XI-01. The following label is being attached: Lectotype of *Erebia mancinus* Doubleday, designated by Jon H. Shepard, 1983. This specimen was photographed by C.F. dos Passos and is illustrated here (figs. 3, 4). The male specimen, labeled: Rocky Mtns., 47-74. Pres. by Lord Derby, is not considered a paralectotype.

The lectotype of *Chionobas chryxus* Doubleday is a female specimen presented in 1845 and labeled: Rocky Mtns., 45-136, type, B.M. Type no. Rh. 3845, *Chionobas chryxus* D. W. & H. ♀. The following label is being attached: Lectotype of *Chionobas chryxus* Doubleday, designated by Jon H. Shepard, 1983. The specimen was photographed by C.F. dos Passos and is illustrated here (figs. 5, 6). The second female specimen, labeled: Rocky Mtns., 45-136, is designated a paralectotype and labeled such.

## ACKNOWLEDGEMENTS

The writing of this paper took an inordinate amount of checking of details which could not have been accomplished without the help of others. Robert Pyle, Greys River, Washington, originally checked the type specimens in the British Museum and located the correspondence of Lord Derby. F.H. Rindge of the American Museum of Natural History provided copies of C.F. dos Passos' photographs of type specimens of these Doubleday names. P.R. Ackery of the British Museum of Natural History re-examined the type series, and attached the lectotype labels. I.D. Wallace, Merseyside County Museum, checked details of Lord Derby's correspondence. D.A.E. Spalding, formerly of the Provincial Museum of Alberta, provided useful information concerning early Alberta naturalists. Charles Bird brought to my attention his work on Thomas Drummond. Judith Beattie of the Hudson's Bay Archives, Winnipeg, is to be especially thanked for the long hours she spent both independently and in helping the author to check many points. Though much of this does not appear in the manuscript, it was all necessary to insure the accuracy of the type locality designation. A.O. Bush and J.A. Powell are thanked for reviewing the manuscript and offering valuable suggestions. The editing skills and

typing efforts of my wife, Sigrid, are greatly appreciated.

#### LITERATURE CITED

- Allen, A.J. 1848. Ten years in Oregon. Mack, Andrus, & Co., Ithaca, N.Y. [I]–XVI, 17–399.
- Barnes, W. and J.H. McDunnough. 1916. Notes on North American diurnal Lepidoptera. Contributions to the Natural History of the Lepidoptera of North America. 3(2): 53–137, pls. 4–11.
- Bird, C.D. 1967. The mosses collected by Thomas Drummond in western Canada. 1825–1827. Bryologist. 70(2): 262–266.
- Britten, James and G.S. Boulger. 1931. A bibliographic index of deceased British and Irish botanists, 2nd ed. revised and completed by A.B. Rendle. Taylor and Francis, London. [I]–XXII, [1]–342.
- Brown, F.M. 1965. The types of Nymphalid butterflies described by William Henry Edwards Part 1. Argynnninae. American Entomological Society, Transactions. 91(3): 233–350.
- Cole, J.M. 1979. Exile in the wilderness. Burns & MacEachern, Lim., Don Mills, Ontario [I]–XVIII, 1–268.
- Doubleday, Edward. 1847–1849. In Doubleday, E., J.O. Westwood, and W.C. Hewitson. 1847–1852. The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus. Longman, Brown, Green, and Longmans, London. Vol. 1: [1]–250, pls. 1–30.
- Douglas, David. 1914. Journal kept by David Douglas during his travels in North America 1823–1827 together with a particular description of thirty–three species of American oaks and eighteen species of *Pinus*. Royal Horticultural Society, London. 1–293.
- Drury, C.M. 1940. Botanist in Oregon 1843–1844 for Kew Gardens, London. Oregon Historical Quarterly. 41(2): 182–188.
- Edwards, W.H. 1891. Description of a new species of *Argynnis* from Alberta Territory. Canadian Entomologist 23(9): 198–199.
- Elwes, H.J. 1889. A revision of the genus *Argynnis*. Entomological Society at London, Transactions. 1889: 535–575.
- Ermatinger, C.O. and James White. 1913. Edward Ermatinger's York Factory Express Journal, being a record of journeys made between Fort Vancouver and Hudson Bay in the years 1827–1828. Royal Society of Canada, Transactions. Ser. 3, Vol. 6, sec. II, 1912: 67–132, 1 map.
- Ewan, Joseph. 1950. Rocky Mountain naturalists. Univ. of Denver Press, Denver, Colorado. [I]–XIV, [1]–358.
- Fletcher, James. 1908. Mountain sprites. Canadian Field Naturalist. 21 (12): 225–231.
- Glover, R.G. 1975. The man who did not go to California. Historical Papers Committee, Canadian Historical Association. 1975: 95–112.
- Gunder, J.D. 1929. The genus *Euphydryas* Scud. of Boreal America (Lepidoptera, Nymphalidae) Pan-Pacific Entomologist. 6(1): 1–8, pls. 1–16.
- Hemming, Francis, 1941. The dates of publication of the specific names first published by Doubleday (Ed.) *Genera of Diurnal Lepidoptera* and in the continuation thereof by Westwood (J.O.). Journal of the Society of Bibliography of Natural History. 1(11): 447–464.
- Kirby, William. 1837. Fauna Boreali-Americana. Vol. 4. Insects. Josiah Fletcher, Norwich,

- England. [I]–XXXIX, [1]–325, +(1), pls 1–7.
- Kohler, Steve. 1980. Checklist of Montana butterflies (Rhopalocera). *Journal of the Lepidopterists Society*. 34 (1): 1–19.
- MacGregor, J.G. 1978. John Rowand. Czar of the Prairies. Western Producer Prairie Books, Saskatoon, Saskatchewan. [I] – (X), [1] – (189).
- Macleod, M.A. ed. 1947. The letters of Letitia Hargrave. The Champlain Soc., Toronto. [I] – CLIV, [1] – 310.
- McKelvey, S.D. 1955. Botanical exploration of the Trans–Mississippi West, 1790–1840. The Arnold Arboretum of Harvard University, Jamaica Plains, Massachusetts. [I] – XL, [1] – 1144.
- Miller, L.D. and F.M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. The Lepidopterists' Society, Memoirs. 2: [I] – VII, 1–280.
- Opler, P.A. 1967. Studies on the Nearctic *Euchloe*. Part 4. Type data and type locality restrictions. *Journal of Research on the Lepidoptera*. 5(3): 190–195.
- Opler, P.A. 1970. Studies on the Nearctic *Euchloe*. Part 5. Distribution. *Journal of Research on the Lepidoptera*. 7(2): 65–86.
- Ormsby, M.A. 1971. British Columbia: a history. The Macmillan Co. Canada Ltd., Toronto, Ontario. [I] – X, [1] – 566.
- Pike, E.M. 1980. Origins of tundra butterflies of Alberta. *Quaestiones Entomologicae*. 16: 555–596.
- Soper, J.D. 1970. The mammals of Jasper National Park, Alberta. Canadian Wildlife Service Report Series. 10: 1–80, map.
- Strecker, Herman. 1882. on *Argynnis astarte* Doubl. – Hew. and other matters. *Entomological News* 3: 218–220.
- Westwood, J.O. 1850–1852. In Doubleday, E., J.O. Westwood, and W.C. Hewitson. 1847–1852. The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations and a catalogue of the species of each genus. Longman, Brown, Green, and Longmans, London. Vol. 2: 251–534, pls. 31–80, 1 supplemental plate.

## BOOK REVIEW: SPOTLIGHT ON THE BUGS

ANDERSEN, N. MOLLER. 1982. *The Semiaquatic Bugs (Hemiptera: Gerromorpha), Phylogeny, Adaptations, Biogeography and Classification*. Entomograph 3, Scandinavian Science Press Ltd., Christiansholms Parallelveg 2, DK 2930 Klampenborg, Denmark. 455 pages, 638 text figures, 16 black and white plates, 3 appendices (names of higher taxa + references; generic names + references; keys to families, subfamilies and genera), Danish summary, bibliography, index. Price D.Kr. 300 (c. \$33.00 USA).

This book treats the higher classification of semiaquatic bugs within the framework of phylogenetic reconstruction. Along the way, Andersen summarizes an encyclopedic knowledge about biology of gerromorphans. In addition to being essential reading for all serious students of Heteroptera, Andersen's monograph is a showcase of how to carry out and present a systematic work which deals primarily with supraspecific taxa. Anyone contemplating a biological investigation involving gerromorphan bugs will want to begin with *The Semiaquatic Bugs*. Anyone looking for a fascinating problem to investigate about evolutionary biology of insects will find a bushelfull while reading this volume.

The six main chapters deal with (1) phylogenetic reconstruction in general, (2) phylogeny of Gerromorpha, (3) character analysis and phylogeny of the higher taxa of gerromorphans, (4) adaptations and ecological diversifications, (5) biogeography and (6) classification. Much of the original data have been used in Andersen's previous publications but they are brought together for the first time in *The Semiaquatic Bugs* and focused on larger questions of phylogenetic relationships and higher classification. In addition to an impressive stack of previous papers dealing with species level systematics of gerromorphan bugs, Andersen has published first-rate papers dealing with life history, wing polymorphism, behaviour and functional anatomy. This unusually wide range of experience is reflected in *The Semiaquatic Bugs* and the resulting perspective will make this work most useful to non-systematists. Andersen writes with attention to problems of interest to experimental and comparative biologists who have little interest in taxonomy *per se*. Andersen's firsthand experience with ecological and behavioural work allows him to insightfully interpret and synthesize data from the literature which are frequently ignored or superficially treated in systematic works.

The writing is clear and concise and Andersen's arguments are easy to follow. When interpretations are tentative and based only upon the most likely interpretation of limited information, Andersen so indicates and often suggests how the situation might be further resolved. The volume is exceedingly well illustrated with an abundance of line drawings in the author's own hand. A reader can come to appreciate the structural diversity of gerromorphans just by flipping through the pages. The plates are of uniformly high quality and photomicrographs are clearly labeled and easy to interpret. However, plates would be easier to use if the corresponding page number had been given along with the text reference. There are few typographical errors and the book is well bound, attractively produced and moderately priced. If similar standards are maintained, entomologists can look forward to future volumes in the Entomograph series with enthusiasm.

The first chapter crisply summarizes Andersen's working principles which are those of contemporary cladistics. This chapter is probably unnecessary for most systematists but, for biologists of other persuasion, it is well at place. It allows the novice to appreciate the assumptions, strengths and weaknesses of Andersen's analysis and, especially, to understand

why the treatment that follows differs from those by previous workers. And, it allows the reader to do so without becoming lost among taxa X, Y, and Z in a dark forest of theoretical cladograms.

In chapter 2 Andersen accomplishes two tasks. First, he explicitly reconstructs the ground plan for the Gerromorpha dealing with traits of eggs, nymphs and adults. An understanding of the ground plan makes subsequent discussion about polarity of character transformation series easy to follow. Second, using the ground plan, Andersen attempts to assess the relationships between gerromorphans and other stocks of Heteroptera. He ultimately agrees with Cobben (1978, *Meded. LandbHoogesch. Wageningen*, 78-5) that gerromorphans are most representative of the ancestral heteropterian stock. However, Andersen clearly establishes the monophyletic nature of the Gerromorpha and concludes that it is the probable sister group of other heteropterian lineages and not a stem group ancestral for the suborder. Among the nine shared, derived traits which define the Gerromorpha, the quadrangular mandibular lever, organization of the pretarsus and the nature of the female gynatrial complex seem most compelling.

Although the task ahead is large, Andersen's detailed discussion leaves the reader optimistic about reconstructing the phylogeny of the Heteroptera through cladistics. Andersen shows well through example that cladistic methods need not fail when confronted with detailed and often incongruent information about distribution of character states. The main lesson is that information about many character systems must be assessed simultaneously. The main working principle is parsimony, *i.e.* the amount of homoplasy (number of convergences and parallelisms evaluated in the context of their evolutionary likelihood) is minimized. Therefore, it is at the level of characters and interpretation that Andersen's phylogenetic arguments are focused. If we aim to seek the best *tentative* explanations and are willing to state and rigorously test hypotheses of cladistic relationship instead of trying to establish links of overall similarity, there are indeed grounds for optimism.

In chapter 3, Andersen summarizes the data base used directly in his phylogenetic reconstruction. This chapter makes up about one half of the text and is a detailed comparison of external and internal anatomy of individuals belonging to each of the 8 recognized families comprising the infraorder Gerromorpha. Significant variation of character states within each family is discussed and each family is diagnosed in terms of shared derived characters. Finally the inferred relationships of subgroups within each family are presented and defended.

I take a few, minor exceptions to Andersen's arguments. For example, it is not clear why a lacinate ovipositor is best interpreted as part of the gerromorphan ground plan, despite its presence in the basal mesoveliids, given that superficial deposition of eggs is also interpreted as the primitive condition for the gerromorphs. Surely some of the lacinate character of the mesoveliid ovipositor must have evolved under selection for improved ability to place eggs within plant tissue. Nor was it clear why the divided gynatrial gland was "inferred to belong to the ground plan of the Gerrinae even if it is not found in all members of the subfamily" (p. 238).

Overall, however, I found Andersen's interpretations well founded and based upon in-depth understanding of the character systems involved. His comparative work with the unique gynatrial complex and with the structure of the metasternal scent glands and associated ducts should inspire additional studies in functional morphology. Insights

obtained about relationships of the highly derived Hydrometridae through analysis of the recently discovered *Velimetra* highlight the great strengths of cladistic analysis. Despite its overall primitive character, *Velimetra* is clearly a cladistic member of the Hydrometridae and this taxon provides a critical link for sorting out the relationships of its highly derived lineage mates. Andersen's analysis of the Gerridae is crisply and brilliantly argued and it differs considerably from that presented recently by Calabrese (1980, *Misc. Publ. Ent. Soc. Am.* 11-5]. Although Andersen's conclusions appear to be based upon a more complete consideration and firsthand analysis of characters relevant to the analysis, it would have been useful had he pointed out the main differences between his results and those of Calabrese and presented explicit arguments that favor his system.

In a short discussion of gerromorphan fossils Andersen points out that the Mesozoic fossil *Engynabis tenuis* Bode may be assigned only speculatively to the Gerromorpha because the specimen does not reveal enough structural detail. Therefore, students of gerromorphan history are left with Tertiary fossils which "represent species typical of their respective groups" and allow only the conclusion that the origin of the Gerromorpha was "probably long before the Tertiary". This conclusion is compatible with the zoogeographic analysis offered in Chapter 5.

The culmination of Chapter 3 is a summary of affinities between families of semiaquatic bugs and a formal reconstruction of their phylogeny. Andersen compares his hypotheses with those advanced by previous authors and, in my opinion, shows that his analysis represents a genuine step forward in understanding. Although Andersen is a faithful cladist and translates branching sequence directly to classification, he is concerned with generation of evolutionary novelty within phyletic lines. In that spirit, Chapter 3 closes with a discussion of "derivation load" in the Gerromorpha and thereby provides an intriguing semiquantitative description of relative divergence for each family. Derivation load is calculated as the percentage of derived characters carried by each taxon and is partitioned into components reflecting (1) divergence of family ground plans from the basal gerromorphan ground plan and (2) amount of divergence encountered within each family. Data presented suggest that although the veliids and hydrometrids have undergone the greatest divergence as a consequence of radiation, other groups such as gerrids and hermatobatids made the most significant leaps in the early stages of becoming independent lineages. It is tempting to suppose that these data provide hints of the historical action of both "gradualistic" and "punctuated" speciation within a single higher taxon.

Semiaquatic bugs have adapted to life on the water surface in a myriad of fascinating ways. In the fourth chapter, Andersen discusses adaptations with respect to habitat selection, locomotion, feeding, flight ability and reproduction. The selective factors seemingly responsible for adaptive trends are identified and relevant ecological investigations are thoroughly reviewed. The adaptive themes are woven together in a scenario which describes significant events in the evolutionary history of the semiaquatic bugs. Andersen argues convincingly that the open water surface has been invaded several times by independent lineages and shows that even marine habitats have been colonized a minimum of four times.

In discussing adaptation for life on the water surface, Andersen provides a basis for isolating significant research problems in evolutionary ecology. For example, males of some tropical gerrid species come in two distinct size classes. Andersen suggests that these represent an extreme form of alternative mating tactics. A study of the genetics of sexual

selection in such a system would surely be fascinating. We also learn that almost nothing is known about factors regulating the size of gerromorphan populations although resource limitation has been often invoked as a mechanism to explain patterns of habitat selection and evolution of wing polymorphism. Andersen makes much of a switch in foraging strategy during evolution of gerromorphs. Although I am convinced that gerrids forage quite differently from their more distant relatives like mesoveliids and hydrometrids, I don't believe that categorization of the more basal families as searching predators and those which have invaded open water ambush predators is appropriate. Yes, gerrids *sometimes* orient to prey by responding to ripple signals but most pond dwelling species generally search actively to find their prey (Spence, 1981, *Ecol.* 62: 1505-14), a large percentage of which are dead arthropods. In more derived gerrid lineages found on flowing water, bugs often position themselves so that the stream acts like a conveyer belt bringing food items to their feet. However, few of the details of gerrid foraging have been worked out.

The most significant aspect of this chapter is that Andersen shows how information, which has been of traditional interest to only ecologists and behaviourists, can be fitted within the framework of phylogenetic systematics. Evolutionary biologists can do much to unravel the complex of selective factors which structure the adaptive themes seen in each lineage. And, it is encouraging that systematists like Andersen are interested in more than coarse speculation about the environmental and behavioural constraints on evolution. Systematic work done in this spirit is likely to attract interest and input from other biologists.

Chapter 5 deals with zoogeography, first with reference to vicariance and dispersal models, and then, by discussing gerromorphan diversity with respect to the major zoogeographical realms. In my opinion, the first section of this chapter was the least successful part of the book. Probably as a result of the apparent great age of gerromorphan families, few clear vicariant patterns emerge at the level of higher taxa and Andersen suggests that present distributions are best explained as reflecting primitive cosmopolitanism with subsequent extinction. A few examples of disjunct distributions of sister taxa are explained as vicariant patterns resulting from continental movement but complete analyses are not offered in this volume. The reader is also presented with examples of widespread species, especially members of *Mesovelgia* and *Microvelia*, which have apparently undergone remarkable range expansion through dispersal. No general theme seems to emerge from the data and analysis presented.

In contrast, the second part of the chapter shows that there are interesting zoogeographical patterns to be explained. For example, the genera of Gerrinae which dominate the northern parts of the world are virtually absent from tropical regions. Faunal diversity is maximum in the tropics and Andersen discusses this empirical observation in light of most theories which have been advanced about latitudinal diversity gradients. Not surprisingly, perhaps, there are little data available to discriminate among hypotheses and most explanations seem potentially satisfactory. Although Andersen mentions that a large portion of the tropical gerromorphan fauna is made up of wingless species, he does not explicitly link this to the idea that tropical diversity has evolved in response to climatic stability. From work reviewed in the contexts of habitat selection and wing polymorphism, we know that wing loss in temperate gerrid species seems to be associated with habitat permanency. This association seems to hold in the tropics where most wingless species occupy flowing water habitats. Zera (1981, *Evol.* 35: 218-225) has shown that low



frequencies of winged individuals in populations of *Gerris remigis* are associated with evolution of genetically divergent local populations. In the climatically stable tropics, wingloss and concomitant genetic isolation could well lead to increased rates of speciation.

The last chapter provides a historical review of the classification of gerromorphan bugs, presents Andersen's new views and briefly characterizes the Gerromorpha with respect to numbers of genera and species. Andersen includes gerromorphan taxa in four superfamilies: (1) Mesoveliodea, (2) Hebroidea, (3) Hydrometroidea and (4) Gerroidea. The chief innovations are recognition of the families Paraphrynoveliidae and Macroveliidae as cladistic members of the Hydrometroidea, the hebrids are seen to be more closely related to the rest of the Gerromorpha than to the mesoveliids, and the madeoveliids are included in the Mesoveliidae. These changes are consistent with Andersen's phylogenetic analysis and seem to be well advised. The chapter also provides a sound basis for organizing the families into subfamilies and tribes. Keys given in appendix III allow identification of the known genera of semiaquatic bugs of the world. The keys worked well for the genera that I had on hand in my collection.

This book is a refreshing exodus from theory bound systematics. However, the study also goes far beyond the usual fare of taxonomic description and evolutionary speculation and grapples with data of interest to a broad range of biologists. As a result, the treatment will stand as a milestone in the study of semiaquatic bugs, even as new trends emerge in theoretical systematics. I attribute the success of this volume to two main factors. First, as a higher taxon, the Gerromorpha includes an unusual amount of structural and lifestyle diversity packaged in a manageable number (c. 1300) of species worldwide. Thus, a treatment can be simultaneously detailed and wide ranging. Second, the spotlight is on the bugs which are obviously Andersen's first academic love. If the book is widely read, and I hope it will be, those of us working on semiaquatic bugs should soon have lots of company.

John R. Spence  
Department of Entomology  
University of Alberta













Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the *Style Manual for Biological Journals*, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English, and one in another language, preferably French.

Tables, including titles and footnotes, must not be more than 7 3/4 X 4 3/4 inches (19.7 X 12.1 cm). Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 3/4 X 5 inches, or 19.7 X 13.2 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, \$17.00 per volume of four issues, normally appearing at quarterly intervals, single issues \$5.00. Back volumes and issues are available at the same cost. There is a postal surcharge of \$4.00 to subscribers outside Canada. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to:

The Editor, *Quaestiones Entomologicae*  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3



3  
4

# Quaestiones

# Entomologicae

A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.

VOLUME 20

NUMBER 2

APRIL 1984



A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 20

Number 2

1984

# CONTENTS

Stanger—Preliminary Observations on Genetic Variations in Three Colonies of <i>Musca domestica</i> (Diptera: Muscidae) Isolated from Central Alberta .....	51
Ratcliffe—A Review of the Penichrolucaninae with Analyses of Phylogeny and Biogeography, and Description of a Second New World Species from the Amazon Basin (Coleoptera: Lucanidae) .....	60
Gooding—Tsetse Genetics: A Review .....	89



PRELIMINARY OBSERVATIONS ON GENETIC VARIATION IN THREE COLONIES OF  
*MUSCA DOMESTICA* (DIPTERA: MUSCIDAE) ISOLATED FROM CENTRAL  
ALBERTA

Jeannette Stanger  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6E 2E3

*Quaestiones Entomologicae*  
20: 51-59 1984

ABSTRACT

Three colonies of house flies, *Musca domestica* L., were established using flies collected from a chickenbarn, a cattle feedlot, and an enclosed pigbarn. (The latter population bred year-round and was insecticide resistant.) Banding patterns on polyacrylamide gel electrophoresis, of heads and thoraces, of adults from these colonies indicated that malic acid dehydrogenase and  $\alpha$ -glycerophosphate dehydrogenase were monomorphic; tetrazolium oxidase, octanol dehydrogenase, and alkaline phosphatase were polymorphic and each was controlled by a locus on an autosome; and glucose-6-phosphate dehydrogenase was polymorphic and controlled by a locus on the X-chromosome. Each of the polymorphic loci had two alleles. Allele frequencies indicated that the colonies were genetically very similar and gave no firm evidence that the insecticide resistant population was genetically isolated from the other populations.

RÉSUMÉ

Trois colonies de mouches domestiques, *Musca domestica* L., ont été établies à partir de mouches prélevées dans un poulailler, un enclos à bétail et une porcherie (la population habitant la porcherie se reproduisait toute l'année et était résistante aux insecticides). Les séries de bandes révélées par l'électrophorèse d'homogénats de têtes et de thorax d'adultes sur gel de polyacrylamide montrent que la déshydrogénase de l'acide malique et la déshydrogénase de l' $\alpha$ -glycérophosphate sont monomorphiques; l'oxydase du tétrazolium, la déshydrogénase de l'octanol et la phosphatase alcaline sont polymorphiques et chacune est sous le contrôle d'un locus situé sur un autosome; la déshydrogénase du glucose-6-phosphate est polymorphique et est sous le contrôle d'un locus situé sur le chromosome X. Chaque locus polymorphique a deux allèles. Les fréquences des allèles indiquent que les colonies sont génétiquement très semblables mais elles ne fournissent pas d'évidence décisive à l'effet que la population résistante aux insecticides est génétiquement isolée des autres populations.

INTRODUCTION

House flies in a colony isolated in 1979 from an enclosed pigbarn near Calmar Alberta, southwest of Edmonton, were resistant to four organophosphate and three pyrethroid insecticides (Harris *et al.* 1982). House flies from the surrounding populations were apparently susceptible to insecticides since they were controlled by insecticide applications. If this resistance were genetically determined by recessive alleles one would expect that the population must be at least partially isolated from the surrounding house fly populations, otherwise the genes for resistance would become diluted due to outbreeding. One way to investigate the extent to which the population in the pigbarn is isolated from the surrounding populations is to compare the allele frequencies at several loci in the resistant population with the corresponding

allele frequencies in the surrounding populations. If the allele frequencies in the pigbarn population are different from those in the other populations in the region this would indicate that the former is, to some extent, genetically isolated from the latter.

The objective of this study was to determine whether the insecticide resistant population of *Musca domestica* L., in the pigbarn referred to above, was isolated from other house fly populations in the area by comparing allele frequencies in colonies established from these populations using polyacrylamide gel electrophoresis.

Ideally such a study should be made by examining flies collected at each of the sites studied, and by examining a large number of loci in each population. However, because this project was part of a course which had to be carried out in the winter months and because no previous work had established methods for storing house flies for subsequent electrophoretic study, I decided to establish colonies from the pigbarn and from two other nearby locations and to electrophorese their descendants. Because of the dearth of information about electrophoresis of *M. domestica* and because of time restraints only six loci were examined.

## MATERIALS AND METHODS

Three populations of house flies, *Musca domestica* L. were sampled August 25, 1981. Colony 1 was established using 300 to 400 flies collected from a pig barn, colony 2 using 50 to 100 flies from a chicken farm, and colony 3 using about 150 flies from a feedlot operation; all occurred within an 8 km radius in the Calmar area southwest of Edmonton Alberta. The pig barn population was in an enclosed structure and was able to reproduce throughout the year. Insecticides were intensively used in this barn and a chronic problem with house flies occurred there. At the time the flies were collected unsuccessful attempts were being made to suppress the population using pyrethroid insecticides. The other two populations were not known to reproduce throughout the year and were presumed to overwinter as hibernating adults or to have been re-established each spring by adults immigrating from winter refugia. Insecticides were occasionally (and successfully) used at the chicken farm and the feedlot, and house flies were not particularly troublesome at either site.

The three colonies were maintained in the culture room at the University of Alberta, Department of Entomology and were used over several generations. The medium for rearing larvae consisted of 100 ml bran, 100 ml wood chips, 25 ml milk powder and 100 ml water. Adults were fed a mixture of dried eggs and sugar, and water was dispensed *ad lib.* through a cotton swab. Eggs were collected every two weeks. Relative humidity in the room varied from 30 to 85%. Lights in the room were controlled on a 14 hour light:10 hour dark cycle.

The procedure and apparatus used for polyacrylamide gel electrophoresis were those described by Gooding and Rolseth (1982), with the following modifications. All of the electrophoretic runs used a 7% gel at pH 8.9. The head and thorax from each fly were homogenized together and there was enough homogenate from each house fly to do two runs. Each gel was stained for one or two of the following enzymes: tetrazolium oxidase (TO), octanol dehydrogenase (ODH), alkaline phosphatase (ALKPH),  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -GPD), glucose 6-phosphate dehydrogenase (G6PD), and malic acid dehydrogenase (MDH) using the methods outlined by Gooding and Rolseth (1982). Four to five months after colonizing the flies, comparisons were made using a minimum of 17 adults from each colony. The comparisons were facilitated by treating samples from two colonies on each gel.

The taxonomic identity of the flies was confirmed by Dr. G.C.D. Griffiths, and voucher specimens were deposited in the Strickland Museum, Department of Entomology, University of Alberta.

## RESULTS AND DISCUSSION

### Electrophoretic patterns and genetic interpretation

For TO, ODH, and ALKPH each fly had either one band or three bands (Fig. 1). This is interpreted as indicating that for each enzyme there is one locus with two alleles, and that the active form of each enzyme is a dimer. Heterozygotes were found in both sexes, indicating that the loci for these enzymes are on autosomes. As far as I am aware this is the first report of an electrophoretic study of ALKPH in *M. domestica*. On polyacrylamide gel electrophoresis two zones staining for TO were reported by McDonald *et al.* (1975). The slower migrating zone appeared to be monomorphic, and the faster migrating zone was controlled by a locus (*To2*) having two alleles (McDonald *et al.* 1975). On the basis of electrophoretic mobility and banding patterns, it is likely that the locus I studied (*To*) corresponds to locus *To2* described by McDonald *et al.* (1975). These authors reported four zones on polyacrylamide gels staining for ODH. Three of the zones were either monomorphic or stained diffusely and were not consistently readable. The locus *Odhl* produced consistently readable bands and had two alleles. It was established, by breeding experiments, that heterozygotes had three bands. Based upon electrophoretic mobility and banding patterns, it is likely the *Odh* locus studied here corresponds to *Odhl* described by McDonald *et al.* (1975).

Each fly had one or three G6PD bands (Fig. 1) and this is interpreted as indicating that this enzyme is controlled by one locus with two alleles, with the active form of the enzyme being a dimer. The locus for this enzyme appears to be on the X-chromosome since no heterozygous males were found (Table I). This enzyme is also known to be on the X-chromosome in tsetse flies (Gooding 1983).

MDH and  $\alpha$ -GPD bands did not vary (Fig. 1). This indicates that each enzyme is controlled by a single locus but its location is unknown since these enzymes were monomorphic.

With the exception of G6PD, phenotype frequencies within each house fly colony indicated that each colony was in Hardy-Weinberg equilibrium at the loci examined (Table I).

### Intra-colony variation

A commonly used measure of genetic variation within a population is heterozygosity. This was estimated in each colony (from data in Table II) as the expected average frequency of heterozygotes per locus (*H*): colony 1,  $H = 19.8 \pm 6.8\%$ ; colony 2,  $H = 10.0 \pm 4.5\%$ ; and colony 3,  $H = 10.9 \pm 6.6\%$ . (Values for *H* and the S.D. were calculated using equations 6.5 and 6.6 from Nei [1975].) Although colony 1 was slightly more heterozygous than colonies 2 and 3, the values obtained for *H* are all comparable to the average values seen in other insect populations. (For examples of *H* values in other invertebrates see Dobzhansky *et al.* [1977, Table 2-9] or Ayala [1982, Table 2.11], and for examples of values found in colonies of tsetse flies see Gooding [1982].)

Field collected *M. domestica* from Mission, Texas had three alleles present at a TO locus and two alleles at an ODH locus (McDonald *et al.* 1975) but the frequencies of these alleles and the heterozygosity at these loci were not reported. Genetic variations of TO and ODH have been studied in two populations collected near Fargo, North Dakota (McDonald and Johnson 1976). Both populations had two alleles at the *To* locus (with the commonest allele being the

same in each population and having frequencies of 88% and 97%). One population had three *Odh* alleles, with frequencies of 4%, 76%, and 20%, while the frequencies of the same alleles in the second population were 0%, 82%, and 18% respectively (McDonald and Johnson 1976). There appear to be no published studies of genetic variation in natural or laboratory populations of *M. domestica* involving any of the other enzymes which I studied. Variation in lactic acid dehydrogenase has been studied in several natural populations of *M. domestica* (Agatsuma and Takeuchi 1976, 1978a, 1978b) and variation in esterases in several strains of house fly has also been reported (Velthuis and van Asperen 1963, Narang *et al.* 1976). Breeding experiments demonstrated hidden heterozygosity on chromosome 3 in a house fly population near Fargo, North Dakota and it was estimated that 23.2% of the individuals carried one or more lethal alleles on chromosome 3 (McDonald and Overland 1974). Using polyacrylamide gel electrophoresis, allele frequencies were determined at six loci and variations, but not allele frequencies, were reported at two other loci in two natural populations of house flies collected near Fargo, North Dakota (McDonald and Johnson 1976). The latter study and the present report seem to be the only quantitative estimates of genetic variation in natural populations or recently isolated colonies of *M. domestica*.

### Inter-colony comparisons

The overall genetic similarity of two populations may be estimated from allele frequencies in those populations by using any of several indices. Using the allele frequency data in Table II and the methods of Nei (1972, 1975) the mean genetic identity (*I*) of the pairs of colonies was estimated to be as follows:  $I(1:2)=0.9937$ ,  $I(2:3)=0.9836$ ,  $I(1:3)=0.9858$ . These values indicate that there were only slight differences between the three house fly colonies and that it is colony 3 (rather than colony 1) which is most different from the other two colonies.

If each of the colonies were established from the same population, and if the allele frequencies within the colonies had not changed due to selection or drift during colonization, one would expect the data to indicate that the population, from which the colonies were established, would be in Hardy-Weinberg equilibrium at each locus. Since the loci for MDH and  $\alpha$ -GPD were monomorphic these loci can not be used in such a test. Nor can the data for G6PD be used since each of the colonies was not in Hardy-Weinberg equilibrium at this locus. For the three enzymes whose loci are on autosomes, analysis of the pooled data indicates that all three are in Hardy-Weinberg equilibrium: for TO  $\chi^2=0.0297$ , for ODH  $\chi^2=0.0052$ , for ALKPH  $\chi^2=0.1042$ ; all  $\chi^2$  values have been calculated with Yates correction for 1 d.f.

Comparing the number of gene products observed in each of the colonies (Table 2) indicated that the three colonies were not significantly different for ODH ( $\chi^2 = 5.8387$ , 2 d.f.) or ALKPH ( $\chi^2 = 5.3082$ , 2 d.f.) For TO there were significant differences among the colonies ( $\chi^2 = 7.4131$ , 2 d.f.,  $0.01 < p < 0.025$ ), and this is largely attributed to the absence of the fast allele from colony 2. There were significant differences in the numbers of each type of G6PD observed in the three colonies ( $\chi^2 = 13.3703$ , 2 d.f.) but the significance of this is difficult to interpret since the colonies were not in Hardy-Weinberg equilibrium at the locus for G6PD.

As indicated above, colony 1 had a greater heterozygosity per locus than did either of the other colonies; the mean for the three colonies was 13.6%. Pooling the phenotype data from all three colonies indicated that the expected average frequency of heterozygotes per locus was 15.6%. These figures indicate that only 13% of the total variation is attributable to variation between colonies (see Hartl 1980).



### General discussion

For reasons stated in the Introduction this study used colonized, rather than field collected, flies. A problem with this approach is that there were opportunities for sampling errors, genetic drift, selection, and inbreeding in the colonies. The colonies were established with reasonably large samples in an attempt to minimize sampling errors at that time. The heterozygosity observed in each colony was comparable to what is seen in naturally occurring populations of insects, indicating that inbreeding had not been severe. It is possible that during the four to 12 generations of colonization there could have been selection or drift which resulted in the colonies becoming more similar to each other than were the natural populations from which they were established. But such an event does not seem likely considering the level of heterozygosity in the colonies.

Overall, the data offer no firm evidence that the colonies were not isolated from the same population. Therefore I tentatively conclude that the insecticide resistant population in the pig barn was either not effectively isolated from the surrounding populations or if it were isolated, the isolation had not been for sufficient time to permit genetic differentiation, at the loci studied, of this population by either drift or selection.

### ACKNOWLEDGMENTS

I thank B.M. Rolseth for assistance in running the electrophoresis, D. Williams for assistance with colonizing the house flies, and Dr. R.H. Gooding for advice during the course of this study and preparation of the manuscript. This study was carried out as part of an Entomology 401 project course and was also supported, in part, by an NSERC grant (No. A3900) awarded to Dr. R.H. Gooding.

### REFERENCES

- Agatsuma, T. and T. Takeuchi. 1976. Genetic control of LDH isozymes in the house fly, *Musca domestica*. *Biochemical Genetics* 14: 441-446.
- \_\_\_\_\_. 1978a. Genetic polymorphism of LDH isozymes in the house fly, *Musca domestica*. I. Seasonal and local variations. *Japanese Journal of Genetics* 53: 367-370.
- \_\_\_\_\_. 1978b. Genetic polymorphism of LDH isozymes in the house fly, *Musca domestica*. II. Geographic cline observed in natural populations. *Japanese Journal of Genetics* 53: 317-325.
- Ayala, F.J. 1982. *Population and Evolutionary Genetics: A Primer*. The Benjamin/Cummings Publishing Co. Inc., Don Mills, Ontario. xiii + 268 pp.
- Dobzhansky, T., F.J. Ayala, G.L. Stebbins and J.W. Valentine. 1977. *Evolution*. W.H. Freeman and Co., San Francisco xiv + 572 pp.
- Falconer, D.S. 1981. *Introduction to Quantitative Genetics*. (Second Edition). Longman, New York. ix + 340 pp.
- Gooding, R.H. 1982. Classification of nine species and subspecies of tsetse flies (Diptera: Glossinidae: *Glossina* Wiedemann) based on molecular genetics and breeding data. *Canadian Journal of Zoology* 60: 2737-2744.
- \_\_\_\_\_. 1983. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). VII. Location of *G6pd* in linkage group I, and *Alkph* in linkage group II. *Canadian Journal*

- of Genetics and Cytology 25: 30–32.
- \_\_\_\_\_ and B.M. Rolseth. 1982. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). VI. Multilocus comparison of three laboratory populations. Canadian Journal of Genetics and Cytology 24: 109–115.
- Harris, C.R., S.A. Turnbull, J.W. Whistlecraft and G.A. Surgeoner. 1982. Multiple resistance shown by field strains of house fly, *Musca domestica* (Diptera: Muscidae), to organochlorine, organophosphorus, carbamate, and pyrethroid insecticides. The Canadian Entomologist 114: 447–454.
- Hartl, D.L., 1980. Principles of Population Genetics. Sinauer Associates, Sunderland, MS, x + 191 pp.
- Levene, H. 1949. On a matching problem arising in genetics. Annals of Mathematical Statistics 20: 91–94.
- McDonald, I.C. and O.A. Johnson. 1976. Isozyme variability studies of translocation homozygotes in the house fly, *Musca domestica* L. Proceedings of the XV International Congress of Entomology, Washington, D.C., pp. 140–145.
- \_\_\_\_\_ and D.E. Overland. 1974. House fly genetics: Variability in a field population. Annals of the Entomological Society of America 67: 359–364.
- \_\_\_\_\_, A.C. Terranova, O.A. Johnson and R.A. Leopold. 1975. Polymorphisms and inheritance patterns of tetrazolium oxidase and octanol dehydrogenase in the house fly. Journal of Heredity 66: 218–220.
- Narang, S., A.C. Terranova, I.C. McDonald and R.A. Leopold. 1976. Esterases in the house fly: Polymorphisms and inheritance patterns. Journal of Heredity 67: 30–38.
- Nei, M. 1972. Genetic distance between populations. American Naturalist 106: 283–292.
- \_\_\_\_\_. 1975. Molecular population genetics and evolution. North-Holland Publishing Company. Amsterdam, Oxford. 288pp.
- Velthuis, H.H.W. and K. van Asperen. 1963. Occurrence and inheritance of esterases in *Musca domestica*. Entomologica experimentalis et applicata 6: 79–87.

Table I  
Phenotypes observed in three house fly colonies.

Enzyme <sup>1</sup>	Colony	s/s	s/f	f/f	H-W <sup>2</sup> $\chi^2$
TO	1	50 (.833) <sup>3</sup>	9 (.150)	1 (.017)	0.746
	2	40 (1.00)	0 (0.00)	0 (0.00)	N.C. <sup>5</sup>
	3	50 (.847)	9 (.153)	0 (0.00)	0.355
ODH	1	2 (.040)	17 (.340)	31 (.620)	0.011
	2	0 (.000)	3 (.176)	14 (.824)	0.103
	3	2 (.071)	13 (.464)	13 (.464)	0.181
ALKPH	1	11 (.647)	5 (.294)	1 (.059)	0.313
	2	14 (.737)	5 (.263)	0 (0.00)	0.341
	3	17 (.944)	1 (.056)	0 (0.00)	0.000
G6PD <sup>4</sup>	1(M) <sup>6</sup>	10 (.370)	0 (.000)	17 (.630)	1.301
	1(F) <sup>6</sup>	1 (.050)	4 (.200)	15 (.750)	
	2(M)	4 (.200)	0 (.000)	16 (.800)	
	2(F)	1 (.053)	2 (.105)	16 (.842)	5.139
	3(M)	1 (.050)	0 (.000)	19 (.950)	
	3(F)	0 (.000)	0 (.000)	20 (1.00)	
					N.C.

<sup>1</sup>MDH and  $\alpha$ -GPD were monomorphic, as indicated in figure 1.

<sup>2</sup>Calculated with correction for small sample size (Levene 1949).

<sup>3</sup>Genotype frequencies are given in parentheses.

<sup>4</sup>Genotype frequencies calculated according to Falconer (1981: 16-18).

<sup>5</sup>N.C., not calculated.

<sup>6</sup>M, male; F, female.

Table II.  
Allele frequencies in three house fly colonies.

Enzyme	Allele <sup>1</sup>	Colony		
		1	2	3
TO	s	0.908 (109) <sup>2</sup>	1.000 (80)	0.924 (109)
	f	0.092 (11)	0.000 (0)	0.076 (9)
ODH	s	0.210 (21)	0.088 (3)	0.304 (17)
	f	0.790 (79)	0.912 (31)	0.696 (39)
MDH	c	1.000 (40)	1.000 (40)	1.000 (40)
$\alpha$ -GPD	c	1.000 (38)	1.000 (38)	1.000 (40)
ALKPH	s	0.794 (27)	0.868 (33)	0.972 (35)
	f	0.206 (7)	0.132 (5)	0.028 (1)
G6PD (F) <sup>3</sup>	s	0.150 (6)	0.105 (4)	0.000 (0)
	f	0.850 (34)	0.895 (34)	1.000 (40)
G6PD (M) <sup>3</sup>	s	0.370 (10)	0.200 (4)	0.050 (1)
	f	0.630 (17)	0.800 (16)	0.950 (19)

<sup>1</sup>Allele designation: s=slow, f=fast, c=common, i.e. only one band observed.

<sup>2</sup>Numbers of gene products observed are given in parentheses.

<sup>3</sup>F=female, M=male.

# Electrophoretic banding patterns in *Musca domestica*

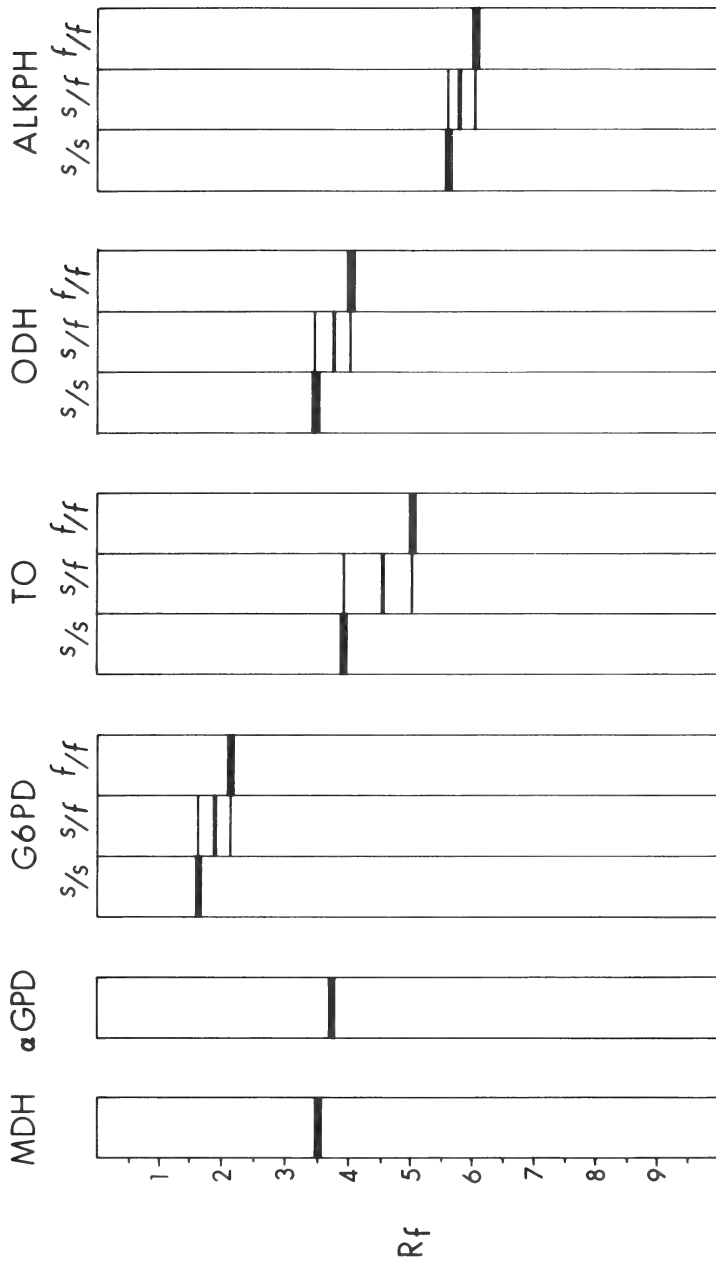


Figure 1. Diagram of the electrophoretic banding patterns observed in *Musca domestica*. MDH, malic acid dehydrogenase;  $\alpha$ -GPD,  $\alpha$ -glycerophosphate dehydrogenase; G6PD, glucose 6-phosphate dehydrogenase; TO, tetrazolium oxidase; ODH, octanol dehydrogenase; and ALKP, alkaline phosphatase.

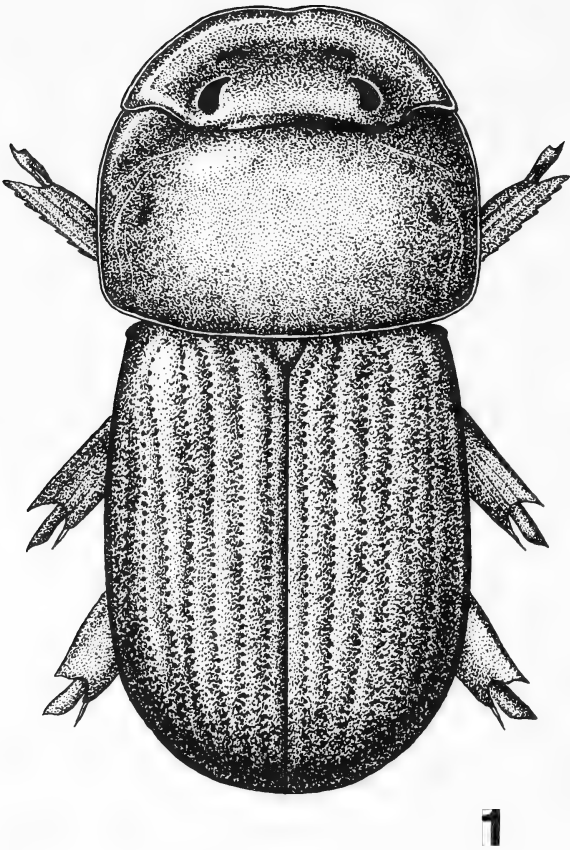


Fig. 1. Habitus of *Brasilucanus acomus* Ratcliffe, new species.

**A Review of the Penichrolucaninae with Analyses of Phylogeny and Biogeography, and Description of a Second New World Species from the Amazon Basin (Coleoptera: Lucanidae)**

Brett C. Ratcliffe

Systematics Research Collections

W436 Nebraska Hall

University of Nebraska State Museum

Lincoln, NEBRASKA 68588-0514 U.S.A.

*Quaestiones Entomologicae*

20: 60–87 1984

**ABSTRACT**

*The Penichrolucaninae is a small subfamily of very rare Lucanidae consisting of Brasilucanus alvarengai Vulcano and Pereira (Brazil, Guyana), B. acomus, new species (Brazil), Penichrolucanus copricephalus Deyrolle (Malaysia), P. elongatus Arrow (Malaysia), P. leveri Arrow (Solomon Islands), P. nicobaricus Arrow (Nicobar Islands), and P. sumatrensis Arrow (Sumatra). A monophyletic origin for the subfamily is indicated because all included taxa share (1) an extremely dorso-ventrally compressed body and (2) fused tarsomeres. No other lucanid adults possess these character states. This paper discusses two alternate biogeographical hypotheses to explain the current distribution of these beetles. The first postulates a Holarctic radiation in the Paleogene with subsequent retreat to tropical refuges in Malaya (post-Miocene) and South America (post-Pliocene). The second postulates a Gondwanan origin and radiation with subsequent vicariance to South America due to continental drift (Upper Cretaceous), dispersal from Africa to Asia (Miocene), and possible extinction in Africa (Miocene onward). A new species of Brasilucanus is described from Amazonian Brazil, a key to genera and species is presented, illustrations of important characters and geographic distribution of taxa are given, and analyses of phylogeny and biogeography are examined.*

**RESUMO**

*Os Penichrolucaninae, grupo pequeno e raro, compreende as seguintes espécies: Brasilucanus alvarengai Vulcano e Pereira (Brasil, Guiana); Penichrolucanus copricephalus Deyrolle (Malásia), P. leveri Arrow (Ilhas Salomão), P. nicobaricus Arrow (Ilhas Nicobar) e P. sumatrensis Arrow (Sumatra). Brasilucanus acomus sp.n. (Brasil, Amazonas) é descrita. Apresento chave de identificação para gêneros e espécies, ilustrações dos caracteres mais importantes, distribuição geográfica e análise filogenética e biogeográfica. Dois caracteres, comuns a todos taxa, indicam a origem monofilética desta sub-família: (1) corpo extremamente comprimido e (2) tarsômeros fundidos. Estes caracteres não aparecem nenhum outro Lucanidae. Duas hipóteses biogeográficas são propostas para explicar a distribuição destes besouros. Na primeira, postulo radiação Holártica durante o Paleogenio com retração subsequente em refúgios tropicais na Malásia (post-Mioceno) e na América do Sul (post-Plioceno). No segundo modelo, proponho origem Gondwanica, com subsequente radiação vicariante à América do Sul devido a deriva continental (Cretáceo Superior), dispersão da África à Ásia (Mioceno) e extinção provável na África (Mioceno, em diante).*

**INTRODUCTION**

The Penichrolucaninae is a distinctive, highly aberrant group of stag beetles. Were it not for their antennae, one would not easily recognize them as stag beetles at all. Moreover, they are exceedingly rare. Based upon collections and literature records with which I am familiar, only

three of the seven known species are represented by more than a single specimen. Penichrolucanines are denizens of dense, equatorial forests in the Amazon Basin, Solomon Islands, and in Malaysia. The locality records (figs. 10-11) represent a disjunct distribution in the extreme. Nothing is known of habits of adults, life cycle, or immature stages of these taxa except that adults of one species were taken in rotting wood. These taxa may be myrmecophilous or termitophilous because penichrolucanine adults show many of the same character states seen in adults of known myrmecophiles such as the paussine Carabidae and the Cremastocheilini of the Scarabaeidae. These states include dorsal-ventral flattening, reduced or compacted tarsomeres and flattened and closely appressed femora. Myrmecophily would also help to explain their current rarity, *i.e.*, they have not been sought out in nests of ants or termites. Based on my own extensive collecting in the type locality of the new species described herein, I believe that adults are not attracted to lights.

Prior to this study, only one specimen had been reported from the New World: the type of *Brasilucanus alvarengai* Vulcano and Pereira. A second specimen of this species was located in the collection at Cornell University. A third specimen, representing a new species from Brazil, is described below.

Arrow (1949) established the subfamily Penichrolucaninae to accommodate five distinctive species in the Malaysian genus *Penichrolucanus*. This genus was formed by Deyrolle (1863) when he described *P. copricephalus* from Malacca (Melaka) in Malaya. Arrow (1935) then described *P. elongatus* from Kuala Lumpur in Malaya, *P. nicobaricus* from Nicobar Island off the northern tip of Sumatra, and *P. sumatrensis* from Palembang in Sumatra. The most recently described Old World species, *P. leveri* Arrow, came from Guadalcanal in the Solomon Islands.

Vulcano and Pereira (1961) briefly reviewed the Penichrolucaninae and described a new genus and species from Jacaré-a-Canga in extreme western Pará state in Brazil, *Brasilucanus alvarengai*. This represented the first reported occurrence of the subfamily in the New World. A second specimen of *B. alvarengai*, this from Guyana, is here reported: "Tumatumari, Potaro R., BR. GUIANA, VI-29-1927, Cornell University, Lot 760, Sub 117." The Guyana specimen clearly indicates that this species occurs both north and south of the Amazon River. Distribution on both sides of the Amazon River is significant from the standpoint of biogeography because the Amazon was a large inland sea during pluvial periods of the Pleistocene (Haffer, 1969; Simpson and Haffer, 1978; Vuilleumier, 1971). Biogeographical data are discussed later in this paper.

The authors of *Brasilucanus* considered it distinct from *Penichrolucanus* because adults of the former genus were characterized by distinct setae dorsally and ventrally, mandibles completely hidden by the clypeus in dorsal view, and greatly expanded and/or shortened femora and tibiae. Discovery of a second species of *Brasilucanus* requires alteration of the generic diagnosis. This is discussed under "Remarks" in the new species description.

I describe below a new species of *Brasilucanus* taken at Reserva Ducke, a forest study site 26 km NE of Manaus, Amazonas, Brazil. This species is the second known from the New World and the first described from a "black water" forest region in the Neotropics.

The Penichrolucaninae, then, consists of two genera with seven species known from approximately 14 specimens. The subfamily was not even reported from the New World until 1961, a fact that is indicative of rarity of these taxa. Consequently, I believe that new taxa may yet be found in South America, Asia, and perhaps also in Africa (see discussion on biogeography).



## Key to Adults of the Penichrolucaninae

- 1 Mandibles completely hidden by clypeus in dorsal view. New World species (*Brasilucanus*) ..... 2
- 1' Mandibles exposed in dorsal view. Malaysian species (*Penichrolucanus*) ..... 3
- 2 (1) Head, pronotum, elytra, and femora setigerously punctate ..... *B. alvarengai* Vulcano and Pereira
- 2' Head, pronotum, and femora glabrous, impunctate ..... *B. acomus* Ratcliffe, n. sp., p. 63
- 3 (1') Elytra lacking punctures on interneurs or on intervals. Color nearly black ..... *P. elongatus* Arrow
- 3' Elytra with interneurs punctate or not and/or punctate on intervals. Color reddish brown ..... 4
- 4 (3') Elytra with interneurs impunctate. Meso- and metatibiae just beyond middle with small spines ..... *P. leveri* Arrow
- 4' Elytra with interneurs punctate. Meso- and metatibiae lacking small spines just beyond middle ..... 5
- 5 (4') Anterior tibia with only small, lateral serrations (fig. 4) ..... *P. nicobaricus* Arrow
- 5' Anterior tibia with distinct, large, lateral teeth (fig. 6) ..... 6
- 6 (5') Mandibles nearly right angled externally ..... *P. sumatrensis* Arrow
- 6' Mandibles not distinctly angulate externally, rounded instead ..... *P. copricephalus* Deyrolle

*Brasilucanus acomus* Ratcliffe, new species

(Figs. 1, 5, 10)

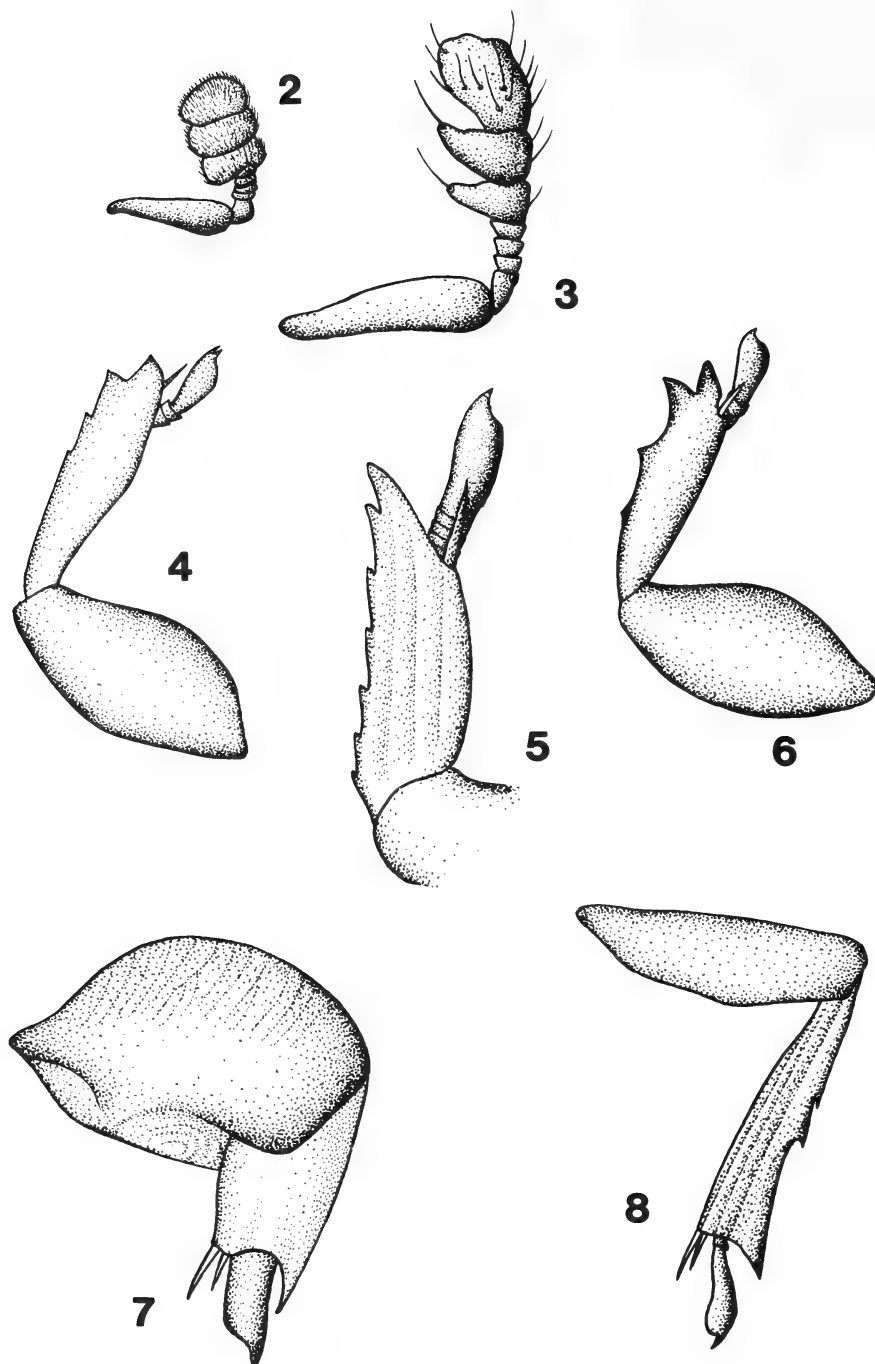
**Type Material.**— Holotype male, labeled "BRASIL, T. Pimental col., Reserva Ducke, Manaus, Am., 4-VII-1970." Type deposited at the United States National Museum.

**Holotype.**— Length 10.1 mm; width across pronotum 5.0 mm; width across humeri 4.4 mm. Body shape rectangular, strongly dorso-ventrally compressed. Color reddish brown, margins piceous. **Head:** Surface smooth, impunctate. Clypeus distinctly, broadly emarginate at center. Eye twice as long as wide in dorsal view. Mentum with disc smooth, impunctate. Antenna with eight segments; club large, loose. **Pronotum:** Surface smooth, impunctate; each side with two extremely fine rugae extended parallel to lateral margin and single ruga extended obliquely across anterior angle from side of pronotum to base of head behind eye. Sides and base with marginal bead, lateral margins broadly explanate. Scutellum small, subsemi-oval. **Elytra:** Surface with six interneurs between suture and humerus; interneurs moderately, deeply impressed, weakly punctate within, punctures obsolete at apical declivity. Intervals smooth, impunctate. Lateral margin narrowly explanate. Humerus with small, feeble tooth externally. **Legs:** Femora and tibiae about 2/3 as wide as long in ventral view; surface impunctate, without setae. Foretibia (fig. 5) with three weak, but distinct, longitudinal ridges on dorsal surface and five or six on ventral surface; apex with two strong teeth, lateral margin with five minute serrations. Foreleg with tarsomeres 1-4 subequal in length, tarsomere 5 longer than rest together. Meso- and metatarsi each with segments fused into single segment.

**Derivation of specific epithet.**— From the Greek *akomos* meaning without hair. So named because of its glabrous body surface (relative to *B. alvarengai*).

**Remarks.**— Adults of *Brasilucanus acomus* are separated from those of *B. alvarengai* by the absence of punctures or setae from head, pronotum, elytral intervals, disc of the mentum, and ventral surfaces of the femora and tibiae.

The generic diagnosis originally given by Vulcano and Pereira (1961) for *Brasilucanus* included setigerous punctures of the dorsum and venter. This distinction is reduced to species-level significance in view of the lack of setigerous punctures on *B. acomus* adults. The



Figs. 2-3. Antennal club of *Penichrolucanus leveri* and *Brasilucanus alvarengai* respectively (after Vulcano and Pereira, 1961).

Fig. 4. Anterior tibia of *Penichrolucanus nicobaricus* (after Arrow, 1935).

Fig. 5. Anterior tibia of *Brasilucanus acomus*.

Fig. 6. Anterior leg of *Penichrolucanus leveri*.

Fig. 7. Posterior leg (ventral view) of *Brasilucanus alvarengai* (after Vulcano and Pereira, 1961).

Fig. 8. Posterior leg (ventral view) of *Penichrolucanus leveri* (after Vulcano and Pereira, 1961).

principal differences between *Brasilucanus* and *Penichrolucanus* are: (1) the mandibles are exposed in *Penichrolucanus* and hidden in *Brasilucanus*; (2) femora and tibiae are very broad in *Brasilucanus* (fig. 7) while much less so in *Penichrolucanus* (fig. 8); and (3) the club of the antenna is consistently more compact and shorter in *Penichrolucanus* (fig. 2) than *Brasilucanus* (fig. 3).

The specimen of *B. acomus* was taken in July during the dry season in this area. It is unknown how the specimen was collected, but it was probably taken from dead wood or by surface gleaning. Light trapping was rarely, if at all, conducted at the type locality in 1970 when the specimen was collected. Moreover, I collected extensively at Reserva Ducke over a two year period with light traps, pitfall traps, and surface gleaning and failed to collect any additional specimens. This attests not only to the rarity of this species but also to the fact that adults do not come to lights.

## SYNOPTIC CHECKLIST OF THE PENICHROLUCANINAE

<i>Penichrolucanus copricephalus</i> Deyrolle 1863: 483.	Malaya
<i>Penichrolucanus elongatus</i> Arrow 1935: 122.	Malaya
<i>Penichrolucanus leveri</i> Arrow 1938: 61.	Guadalcanal, Solomon Islands
<i>Penichrolucanus nicobaricus</i> Arrow 1935: 123.	Nicobar Islands
<i>Penichrolucanus sumatrensis</i> Arrow 1935: 124.	Sumatra
<i>Brasilucanus alvarengai</i> Vulcano and Pereira 1961: 475.	Amazonian Brazil, Guyana
<i>Brasilucanus acomus</i> Ratcliffe, n. sp. 1984: 63.	Amazonian Brazil

## PHYLOGENY

### Introduction

Phylogenetic relationships among these stag beetles have not been previously addressed. Indeed, the higher classification of the Lucanidae in general is unsettled (Holloway, 1960; Moore, 1978). I believe, however, that it is not premature to propose such relationships even though data for these organisms are few. It may even be advantageous to formulate such a relationship hypothesis now to stimulate further interest in these elusive beetles. Assuming further specimens and data are forthcoming, then our phylogenetic considerations will grow by accretion. The added benefit of this is, of course, that new data will provide a test of congruity for any preceding hypothesis. I propose a hypothesis of relationship based upon which animals share derived states of the same homologous character (synapomorphies). The operational philosophy for establishing this hypothesis is that of Hennig (1966) and the many subsequent developers of cladistic methods.

### Character Analysis

Adults within this subfamily all share peculiar modifications. The independent appearance of these non-lucanid structures in two separate groups of Lucanidae seems extremely improbable and so the Penichrolucaninae are viewed most parsimoniously as a monophyletic lineage. The characters that bind the taxa together in a phylogenetically unified lineage are: (1) the dorso-ventrally compressed body; and (2) the peculiar form of the tarsomeres which are fused into a single segment in the meso- and metatarsi. No other lucanid adults possess body form and tarsal characters like those seen in the Penichrolucaninae. Because penichrolucanines are so unique, they warrant subfamily status as proposed by Arrow (1949) and reiterated by

Benesh (1960). Didier and Séguéy (1953) (possibly only following Roon [1910]) placed the penichrolucanines in the Figulinae, but I cannot agree with this because of their unique characters.

Characters and their states were derived from specimens of *Brasilucanus* and *Penichrolucanus* and from a careful analysis of the literature for *Penichrolucanus*. There is an inherent disadvantage in obtaining character data from literature sources, particularly when descriptions are brief or do not describe the same characters. Fortunately, a single author described all but one of the *Penichrolucanus* species, and these narratives were detailed enough to establish character states. Three species on the cladogram lack apomorphies, and this is attributed to failure to find suitable characters because of a lack of specimens in series from which to glean data. Four of the seven species are known from only a single specimen. I believe that synapomorphies do exist for these species, but that more material for study is necessary to ascertain what they might be.

The out-group method of Watrous and Wheeler (1981) was used to polarize characters into ancestral and derived states. The sister group of the Penichrolucaninae has not been identified. Character polarizations were based largely on the Figulinae as the out-group because the Figulinae share more morphological affinity with the Penichrolucaninae than any other subfamily. While this may not show relationship in and of itself, it is suitable for the comparisons of characters. The remainder of the Lucanidae was used as the broader out-group when both states of a character were encountered in the Figulinae. Characters and their polarities are shown in Table 1.

## Characters

Distinctly depressed body form (apotypic state of character 1) and fused tarsomeres in the meso- and metatarsi (apotypic state of character 2; figs. 7-8) are possessed by all the taxa in this group, and this binds them together in a monophyletic lineage. No other lucanid adults possess these character states. The gena (character 3) is greatly expanded and laterally flared, and this is viewed as apotypic. All species have this character state except *P. leveri* which has secondarily lost it. Eyes (character 4) are interpreted for these beetles as derived when dorsally large as in *Penichrolucanus* as opposed to the small eyes of *Brasilucanus*. Small eyes in lucanids are not always plesiotypic as exemplified by South African *Colophon* species which have secondarily reduced eyes and wings and are restricted to mountain summits. Mandibles (character 5) are exposed in all lucanid adults except those of *Brasilucanus*, a state that is interpreted as plesiotypic for *Penichrolucanus*. Hidden mandibles in *Brasilucanus* are unique and, therefore, apotypic. The presence of two tubercles on the head (character 6) in *P. nicobaricus* and *P. sumatrensis* is synapotypic. The figuline *Caprinigidius trifurcatus* Didier and some species of *Figulus* possess one or three tubercles on the head, but a bituberculate head is lacking. A small, compact antennal club (character 7; fig. 2) is plesiotypic (*Penichrolucanus*), and a more open, looser club (fig. 3) is apotypic (*Brasilucanus*). The more primitive scarabaeoid adults have a small, compact antennal club.

The apex of the protibia (character 8) is autapotypically bifid (fig. 4) in *P. nicobaricus*; this form of tibial apex was not seen in the Figulinae. Large, distinct, external teeth on the protibia (character 9; fig. 6) is considered apotypic on an *ad hoc* basis. Absence or presence of such teeth are both widespread in the family, and a more detailed analysis needs to be undertaken in order to resolve this polarity problem.

Table 1. Penichrolucaninae characters: plesiotypic and apotypic states.

No.	Character	Plesiotypic	Apotypic
1	Body convexity	convex	depressed
2	Tarsomeres	segments normal	segments fused
3	Gena	normal, rounded	laterally expanded
4	Eye size	small	large
5	Mandibles	exposed	covered
6	Tubercles on head	absent	present
7	Antennal club	small, compact	large, loose
8	Protibial apex	not bifid	bifid
9	Protibial teeth	weak, small	strong, large
10	Mid-metatibial teeth	absent	present
11	Width of femora	slender	broad
12	Width of tibiae	slender	broad
13	Metatibial length	long	very short
14	Pronotal punctation	present	absent
15	Punctuation of interneurs	absent	present
16	Dorsal setae	absent	present

I interpret the presence of several small teeth just behind the middle of the meso- and metatibia (character 10) as apotypic, a state present in all the penichrolucanine taxa except *P. leveri* (which is geographically isolated in the Solomon Islands) and *Brasilucanus*. Extremely wide femora (relative to length; character 11; fig. 7) are apotypic in *Brasilucanus* because no other lucanids possess such highly aberrant femora. Similarly, the marked width of the tibiae (relative to length; character 12; fig. 7) is apotypic as opposed to the more conventional, slender lucanid tibiae (fig. 8). All *Penichrolucanus* adults, except those of *P. leveri*, show a slight widening of the tibiae that becomes even more derived in *Brasilucanus*. Length of the metatibia (character 13) is considered apotypic when it is very short, and this constitutes a reduction of a once longer tibia. Only *P. elongatus* retains this character in a plesiotypic state. The tibia is considered long if its inside length is at least as long as the length of the pronotum.

The absence of pronotal punctures (character 14) is autapotypic and is seen only in *B. acomus*. The remainder of the Penichrolucaninae, as well as the outgroup, possess distinct pronotal punctation to some degree. Punctuation within the elytral interneurs (character 15) is plesiotypic because this character is commonly found in the out-group. The presence of pronotal and elytral setae (character 16) is rare in the Lucanidae; presence of setae in *B. acomus* is autapotypic within the Penichrolucaninae.

### Phylogenetic Relationships

In table 2 are listed the character state distributions for the taxa of Penichrolucaninae. A cladogram was produced (fig. 9) based on this set of character state distributions. The cladogram was constructed using the assumption that the most parsimonious arrangement of shared, derived character states with the fewest homoplasies (parallelisms, reversals) best infers genealogical relationship.

Table 2. Characters and Distribution of Phylogenetically Classified Character States<sup>1</sup> among the Species of *Penichrolucaninae*

No.	Character	Species <sup>2</sup> and Character States						
		aco	alv	nic	cop	eln	sum	lev
1	Body convexity	1	1	1	1	1	1	1
2	Tarsomeres	1	1	1	1	1	1	1
3	Gena	1	1	1	1	1	1	0
4	Eye size	0	0	1	1	1	1	1
5	Mandibles	1	1	0	0	0	0	0
6	Tubercles on head	0	0	1	0	0	1	0
7	Antennal club	1	1	0	0	0	0	0
8	Protibial apex	0	0	1	0	0	0	0
9	Protibial teeth	0	0	0	0	0	1	0
10	Mid-metatarsal teeth	0	0	1	1	1	1	0
11	Width of femora	1	1	0	0	0	0	0
12	Width of tibiae	1	1	1	1	1	1	0
13	Metatarsal length	1	1	1	1	0	1	1
14	Pronotal punctation	1	0	0	0	0	0	0
15	Punctation of interneurons	1	1	1	1	0	1	0
16	Dorsal setae	0	1	0	0	0	0	0

<sup>1</sup>Scores for character states: 0 = plesiotypic; 1 = apotypic.

<sup>2</sup>Abbreviations for specific epithets: aco = *acomus*; alv = *alvarengai*; cop = *copricephalus*; eln = *elongatus*; lev = *leverii*; nic = *nicobaricus*; sum = *sumatrensis*.

Ranking of *Brasilucanus* and *Penichrolucanus* as genera is justified because the phyletic distance between them is broad; *Brasilucanus* has significant character states not shared by *Penichrolucanus*. It is not surprising that the two New World species have the most synapotypies, and it is not surprising that they cluster as sister species.

*Penichrolucanus leverii* retains the most ancestral character states in the Old World taxa, which is in keeping with isolation and severely restricted gene flow from the parent stock in the region of the Malay Peninsula. The reduced genetic interchange in such isolated taxa permits retention of more ancestral character states. The four remaining Old World species are more derived than *P. leverii*, more tightly clustered geographically, and probably have experienced greater or more recent gene flow amongst themselves. *Penichrolucanus nicobaricus* is not excluded from this interchange because the islands on which it occurs are not remote, isolated, oceanic islands but share the Asian continental shelf with the Malay Peninsula and Sumatra. Based on the current, limited data, synapotypies were not found for *P. copricephalus*. In spite of this, I have formed the cladogram to reflect what I believe to be the correct branching sequence for this species instead of showing its node as a trichotomy with *P. nicobaricus* and *P. sumatrensis*. This *ad hoc* hypothesis can be tested when further character data become available.

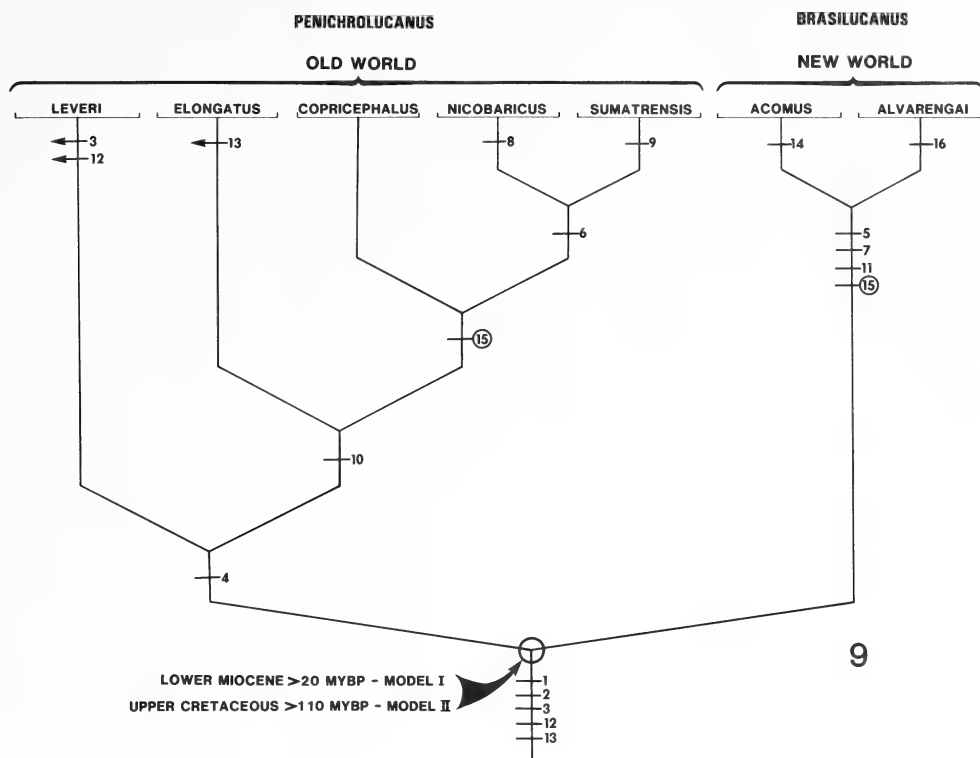


Fig. 9. Cladogram with proposed genealogical relationships of the species of Penichrolucaninae. Numbers refer to apotypic characters; horizontal lines indicate character advancement; arrows show character reversals.

## BIOGEOGRAPHY

*Life, unlike the inanimate, will take the long way round to circumvent barrenness* --- L. Eisely.

*Penichrolucanus* and *Brasilucanus* are separated from one another by a world. How did this disjunct distribution happen given the monophyletic origin of the lineage? Fossil Penichrolucaninae are unknown, and it is not unreasonable to predict that they probably never will be found. Without fossil data, it becomes necessary to use a synthesis of data from plate tectonics, present and paleodistributions of other plants and animals, and phyletic relationships within the penichrolucanines to formulate a model to best explain the current distribution of these beetles. "It is a normal practice in science to infer from what is better and more completely known in order to discover the structure and the meaning of that which is less well or only partly known. The similarity of facts known on both sides of a controversy suggests that the best documented will be taken as a good model for the reconstruction of the structures still unknown on the other side" (Lavocat, 1980: 93). Ball (1975) also advocates deductive approaches to biogeographical reconstructions rather than narrative, inductive methods. I have



Fig. 10. Distribution of the species of *Brasilucanus*.





Fig. 11. Distribution of the species of *Penichrolucanus*.

attempted to follow these precepts.

Distribution of the Penichrolucaninae is shown in figs. 10-11. *Brasilucanus* is Neotropical, and *Penichrolucanus* is tropical Asian with one species crossing Wallace's Line to the Solomon Islands in the western Pacific. Two quite different models are proposed to explain the current distribution of these beetles. Each model is a maximum parsimony hypothesis, congruent with the cladogram, and is a blend of vicariance and dispersal paradigms of biogeography. Plate tectonics, as exemplified by sea floor spreading and continental drift, is implicitly assumed in this study.

### Model I: Holarctic Origin

Within the framework of this model, the synthesis of data from other plants and animals, geology, and paleoclimatology favor the basal stock of the Penichrolucaninae being present in Holarctica, specifically either North America or eastern Asia, at least prior to the middle Miocene approximately 20 MYBP (million years before present) (figs. 12-13). Whether ancestral penichrolucanines originated in Asia or North America is unknown and probably unresolvable. It is of interest to note that North America has eight genera of Lucanidae, Latin America has 16 genera, Africa has nine genera, and Asia has 37 genera (Roon, 1910). Similar large differences favoring Asia at the species level are also present. Origins aside, it seems that the greatest *radiation* of Lucanidae has been in Asia.

Dispersal of ancestral Penichrolucaninae via Beringia occurred from Asia to America or *vice versa*. MacGinitie (1969), citing the distinct subtropical Asiatic element in the Eocene flora of the west coast of North America typified by the genera *Alangium*, *Canarium*, *Cinnamomum*, *Columbia*, *Cryptocarya*, *Mastixia*, *Neolitsea*, *Phytocrene*, and *Terminalia*, concluded that there must have been active dispersal around the northern Pacific in the early Tertiary. He continued by noting that this dispersal route is further indicated by the genera *Acalypha*, *Cissampelos*, *Chrysophyllum*, *Lucuma*, *Meliosma*, *Symplocos*, and others which occur as fossils in the Goshen and La Porte floras and which are both Neotropical and Paleotropical in their present distribution. This distribution suggests strongly a much wider area of occupancy in the past, and this and similar evidence led MacGinitie (1969), Leopold and MacGinitie (1972), Dorf (1957) and others to conclude that a large area of subtropical to tropical forests once extended from the American tropics around the northern Pacific to the Asian tropics during the Paleogene.

There exists a distinct faunal similarity (suggesting warm climates) within the vertebrates between Asia and North America by the middle Miocene (proboscideans, primates, *Alligator*). Tapirs (order Perissodactyla) provide strong evidence for a subtropical to tropical dispersal route around the northern Pacific. Tapirs are and were primarily warm climate animals and are the only extant mammals found exclusively in the Asian and American tropics. Penichrolucaninae are also found only in the Asian and American tropics. Fossil evidence indicates tapirs were once much more widespread than they are today. Early tapiroids are found in Eocene and Oligocene deposits in North America, Mongolia and Korea (Radinsky, 1963), and true tapirs are found in the Miocene and later of Eurasia and North America (Romer, 1945; Schultz *et al.*, 1975). Tapir evidence indicates that there was good faunal interchange between North America and Asia in the late Eocene to early Oligocene. A complex pattern of alternating periods of faunal linkage and isolation between these two areas began in the Oligocene due to climatic changes and fluctuations in sea levels (Colbert, 1974; Cox, 1974). Beginning in the mid to late Miocene, climatic conditions were becoming too cool to permit

<b>Cenozoic</b>	<b>Quaternary</b>	<b>Pleistocene and Recent</b>	<b>1.8</b>
		<b>Pliocene</b>	<b>7</b>
	<b>Tertiary</b>	<b>Miocene</b>	
			<b>26</b>
		<b>Oligocene</b>	<b>37.5</b>
		<b>Eocene</b>	
<b>Mesozoic</b>			<b>53.5</b>
		<b>Paleocene</b>	<b>65</b>
	<b>Cretaceous</b>	<b>Upper Cretaceous</b>	
			<b>100</b>
		<b>Lower Cretaceous</b>	
			<b>136</b>
	<b>Jurassic</b>	<b>Upper Jurassic</b>	
			<b>162</b>
		<b>Middle Jurassic</b>	<b>172</b>
		<b>Lower Jurassic</b>	
			<b>192.5</b>
<b>Paleozoic</b>	<b>Triassic</b>	<b>Upper Triassic</b>	
			<b>205</b>
		<b>Middle Triassic</b>	<b>215</b>
		<b>Lower Triassic</b>	<b>225</b>
	<b>Permian</b>	<b>Upper Permian</b>	<b>240</b>
		<b>Lower Permian</b>	<b>280</b>

Fig. 12. Geologic time scale from Permian to present. Numbers at right refer to age at beginning (MYBP). (after Seyfert and Sirken, 1973).

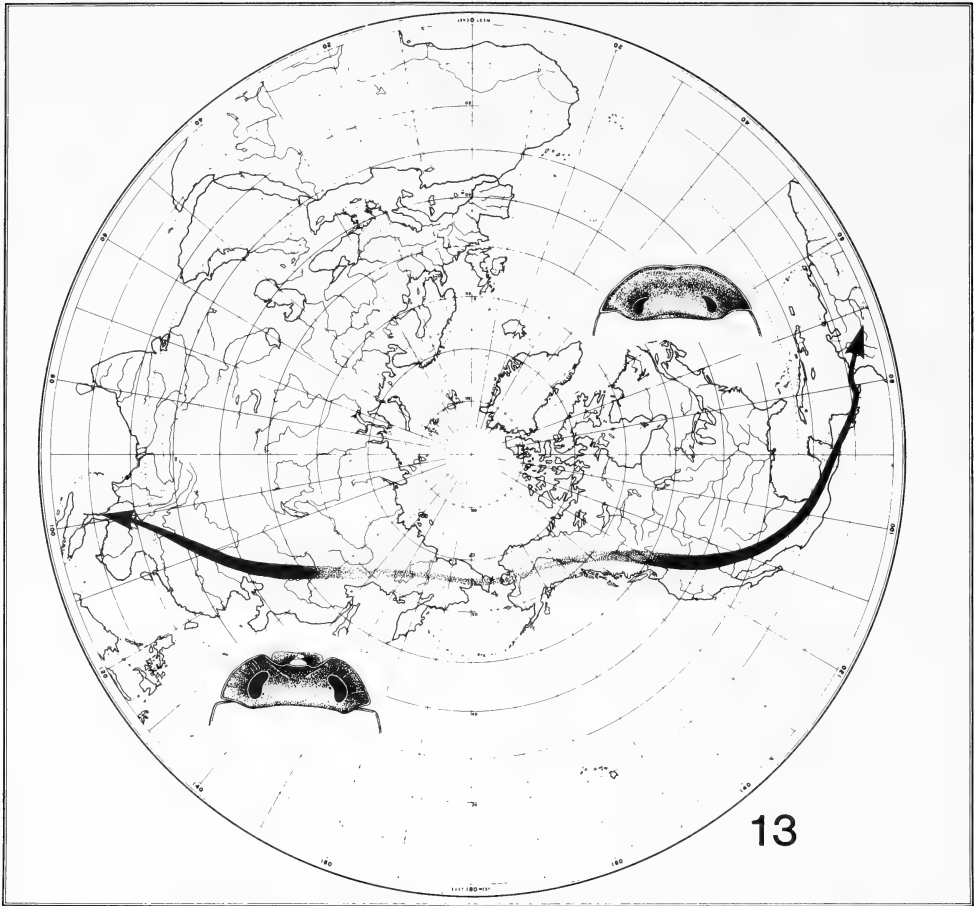


Fig. 13. Model I interpretation of biogeography showing generalized track of initial Holarctic radiation with subsequent retreat to tropical Malesia and tropical South America. Heads shown are *P. sumatrensis* and *B. acomus*.

dispersal of subtropical to tropical organisms between northern Asia and America (Michael Voorhies and Robert Hunt, personal communication, 1983). Warm climate plant and animal taxa retreated southwards. Tapirs, and presumably ancestral penichrolucanines, became extinct by the Pleistocene in what is now north temperate Asia and America, but they continued as relictual populations in tropical Asia and America.

In Asia, tapirs (one species) and penichrolucanines (five species) found refuge largely in tropical Malaya. In the New World, tapirs (three species) and penichrolucanines (two species) retreated southward to Central and South America. The closure of the Bering land corridor (due more to climate than physiography) marks the point of the *Brasilucanus*/*Penichrolucanus* dichotomy. All subsequent evolution of the *Brasilucanus* lineage in North America and their

eventual dispersal into South America would have occurred as an independent and parallel event to the evolution of the *Penichrolucanus* lineage in Asia and its dispersal into Malaya.

I believe this model acquires added significance because of the similarities (distribution, climatic and habitat requirements) between these beetles and the tapirids. Tapiridae have a known fossil record which enables reconstruction of their history, and the similarities allow for cautious extrapolation to the Penichrolucaninae. Tapirid history (as well as that for many other Eurasian-American animals and plants) clearly indicates dispersal via Beringia to explain the overall pattern in distribution of higher taxa. Intracontinental vicariance can then account for many of the distributions of the lower ranking taxa.

*New World.*— Tapiridae penetrated South America in the late Pliocene (Keast, 1972a) in separate invasions at widely separated periods when climates and topographic features were different (Hershkovitz, 1972). About half of the extant Neotropical genera of mammals are derived from late Pliocene or Quaternary North American invaders (Keast, 1972a). Pre-Miocene dispersal of vertebrates between North and South America occurred probably uncommonly through a filter route according to the fossil record. This reduced amount of interchange agrees with the geologic evidence suggesting a relatively wide separation of the Americas in Cretaceous through Oligocene times (Gose *et al.*, 1980; Raven and Axelrod, 1974; Smith and Briden, 1977). An extensive faunal exchange occurred from the Pliocene on as Mesoamerica coalesced from a peninsula and islands (Woodring, 1954) comprising a sweepstakes dispersal route to a definite land bridge in the Pliocene approximately 5.7 MYBP (Lloyd, 1963). Formation of just such a dispersal route allowed for entry into South America of Nearctic, ancestral penichrolucanines.

The modern mammalian fauna of the Amazon Basin seems derived from the Brazilian and Andean uplands (Hershkovitz, 1972). Similarly, Camp (1952) stated that the flora of the central Amazon Basin was derived from surrounding uplands, and that it is a recent flora (late Pliocene or Pleistocene) characterized by many groups with often inadequately delimited genera and species. The relatively recent nature of the largely upland-derived fauna and flora is partially a result of the periodic marine transgressions in the Amazon Basin during the Pliocene and pluvials of the Pleistocene. Post-inundation, hence recent, invasion of the Central Amazon valley by Penichrolucaninae is indicated. The South American collecting sites for these beetles are all less than 100 meters in elevation and were probably submerged at times of high water during the Tertiary/Quaternary transition.

Lastly, the proposed Amazonian forest refugia of the Pleistocene (Brown *et al.*, 1974; Brown, 1977; Haffer, 1969, 1978, 1982; Müller, 1973; Prance, 1973, 1982; Simpson and Haffer, 1978; Tricart, 1974; Vuilleumier, 1971) undoubtedly affected penichrolucanine beetles. The refuge theory, in essence, states that during the Quaternary, lowland rain forests contracted during dry periods (glaciations usually) while savannas and other nonforest biotopes expanded. During wetter times the rain forests again expanded, and the nonforested grassland regions contracted. Each of the periods of the contraction can be viewed as a vicariance event that led to certain extinction for some species and potential speciation within other taxa. Subsequent expansion of forests allowed dispersal of previously isolated taxa. Duellman (1982), Livingstone (1982), Lynch (1982), and especially Endler (1982a, b) question the refuge theory and suggest that events other than Pleistocene forest contractions and expansions could be responsible for the present day diversity and distributions of the descendent tropical biota. Although distribution of a taxon in and of itself is inadequate support for the refuge theory, the increasing evidence provided by geomorphology, palynology, and paleoclimatology give

additional credence to this interpretation.

Penichrolucanine beetles are extremely rare today. Severe disruption of a formerly more continuous range during Pleistocene times due to climatic change accords well with their patchy distribution and rarity. The present distribution of *Brasilucanus* has a remarkable similarity to Haffer's (1969) bird refuges, Prance's (1982) angiosperm refuges, and to the Pleistocene vegetational refuges proposed by Ab'Sáber (1982) which were based on geological, climatological and pollen data. Penichrolucanines may be patchy in their distribution because they have not been able to disperse far from their hypothetical Pleistocene refuge areas where they occur today as endemic relicts. Failure to colonize or re-colonize after Pleistocene disruption of habitat or competitive exclusion by other animals would both help to account for current patchiness and rarity. New discoveries of *Brasilucanus* in South America would provide much needed additional data with which to test these suppositions. Even though the correlation between these proposed refuges and the distribution of *Brasilucanus* is tantalizing, I feel that these centers of diversity and endemism require further paleontological evidence to prove that they are indeed the result of Pleistocene refugia.

*Asia*.— While dispersal from the Holarctic source area may have begun in the late Eocene to early Oligocene, arrival at and radiation in the Sunda region was a later event. Establishment of Penichrolucaninae in Malaya and Sumatra by at least Miocene times is considered tenuous because much of this region was not even permanently emergent until the Miocene when the northward-moving Australian plate arrived in the vicinity of the Asian plate (Beaufort, 1951; Raven and Axelrod, 1972, 1974; Schuster, 1972; Umbgrove, 1938).

Sumatra, Java, and Borneo are separated from one another and from mainland Asia by shallow seas, many less than 100 meters in depth. Pacific sea levels fell as much as 100-180 meters below present depths during Pleistocene glacial maxima (Audley-Charles and Hooijier, 1973; Biswas, 1973; Geyh *et al.*, 1979; Keast, 1972b; Kuenen, 1950; Verstappen, 1975; Walker, 1982), and much of today's Sunda and Sahul island region was interconnected by dry land or by much larger islands with smaller water gaps. Ancestral Penichrolucaninae would have been able to disperse from mainland Asia over a land corridor or by a series of island stepping stones to the Sunda region. This is certainly so for many vertebrates (Sartono, 1973). Proboscideans, for example, dispersed from Indomalaya to Java, Borneo, Celebes, and Timor (Hooijier, 1967) and even to Mindanao and Luzon in the Philippines (Johnson, 1980). Fossil hippopotomids and giraffids are also known from the Pleistocene of Java (Hooijier, 1975; Keast, 1972b; Medway, 1972). Further, plant geographers have considered the ranges of the Southeast Asian endemic Dipterocarpaceae as good indicators for the existence of former land connections because of their limited powers of seed dispersal (Meijer, 1974). The subsequent rise of sea levels to current depths then fractured and isolated populations, restricted gene flow, and contributed to speciation in the biota of the entire Malayan region.

During the Pleistocene dry cycles, the Malesian<sup>1</sup> islands preserved a great part of the widespread mid-Miocene tropical flora (Meijer, 1982) and presumably fauna. There is growing evidence to indicate that during this period the lowland dipterocarp forests of the Malay Peninsula, Borneo, and Sumatra were preserved as a humid refuge surrounded on the east by

---

<sup>1</sup>"Malesia", a Dutch term, is used for the area including Malaya (south of the Kra isthmus) and the islands commonly referred to collectively as the Indo-Australian Archipelago. This usage of Malesia in biogeography follows Walker (1982: 559, Fig. 30.4) and others.

an arid corridor which extended from Celebes to Java and the Lesser Sunda Islands (Meijer, 1982). This proposed plant refuge corresponds with the present distribution of the Penichrolucaninae in Malesia just as there is a similar conjunction of these beetles and proposed refuges in the Neotropics.

In view of documented swimming powers of modern elephants, Johnson (1980) argued cogently that historical insular biogeographies (such as in Malesia) may have to be re-evaluated, particularly when these reconstructions depend on the presence of proboscideans (again, as in the East Indies) to imply land bridges. The hypothesis proposed here does not require land bridges but only significant narrowing of water gaps. In so doing, the hypothesis of dispersal becomes not only more parsimonious, but also much more likely to have actually occurred. This is, I believe, in accord with known historical geology for the region and accommodates Johnson's concern for insular paleogeographic scenarios using proboscidean data.

The predominantly tropical fauna of the Sunda region is continental Asian almost completely and demonstrates clearly the pathway the Penichrolucaninae used to reach Sumatra, the continental Nicobar Islands, and possibly other areas in the Greater Sunda Islands and the Moluccas. Additional taxa of these beetles may yet be awaiting discovery in this region as well as in mainland Indochina.

*Western Pacific.*— *Penichrolucanus leveri* occurs on Guadalcanal in the Solomon Islands. The Solomons are an oceanic archipelago and have never been connected with New Guinea or the Indonesian islands to the west. This island arc evolved from a series of oceanic, volcanic welts which started to shoal in the Miocene (Hackman, 1971; Quantin, 1971; Tarling, 1971). Due to their late origin, the biota of these islands has a distinct immigrant pattern of dispersal of Indomalesian taxa which were carried to the Solomons across water barriers and *via* New Guinea (Darlington, 1957; Keast, 1972b; Raven and Axelrod, 1972).

Many lucanids seem to be good overwater dispersers (Howden, 1981) and one monobasic genus, *Apterochylus* Waterhouse, has even reached the Hawaiian Islands. The prevailing modern surface currents for the East Indies are essentially from Malaya, Sumatra, and Borneo eastward toward New Guinea, the Bismarks, and the Solomons. It is postulated that ancestors of *P. leveri* rafted to the Solomons from the Malayan source area. This reconstruction implies that actual over water dispersal would need to occur only from the then terrestrial, confluent Greater or Lesser Sunda Islands on the Asian continental plate across the Banda Sea to New Guinea on the Australian continental plate and then to the Solomons. The rationale for this route is that lowered sea levels during the Pleistocene permitted terrestrial (or nearly so) connections among many of the Malesian islands. Considering that Guadalcanal is Miocene in age, then colonization must have occurred later than this. It could be inferred that this colonization was not a recent event because the primitive character states retained by this species suggest long isolation from the parent stock.

## Model II: Gondwanan Origin

This model proposes that the Penichrolucaninae are a much older lineage with origin and initial radiation in Gondwanaland. This would have happened at least prior to 110 MYBP which coincides with the early Albian break between Africa and South America (Dietz and Holden, 1970; Tarling, 1971; Veevers *et al.*, 1971). Although fossil plant and animal data tend to support this hypothesis, the fact remains that these beetles are unknown in Africa. This does not necessarily falsify the model of origin, but makes it slightly less acceptable in view of the

weight of the present evidence. It is presented as an alternate hypothesis based on the contingency that penichrolucanines now inhabit or once inhabited Africa. Figures 14-16 show the position of the continents resulting from drift and illustrate how ancestral Penichrolucaninae became isolated from one another.

*South America.*— The ancestors of *Brasilucanus* became separated from the African penichrolucanines by the rifting between South America and Africa. Ancestral *Brasilucanus* evolved in isolation during South America's long westward drift and developed unique character states not found in other members of the subfamily. As explained previously in the first model, Pleistocene forest refugia may have been the principal means by which the Penichrolucaninae survived in South America during past times of great climatic and ecological disruption. Hypothetical African taxa may not have been so fortunate.

*Africa.*— Penichrolucaninae are not known from Africa. Within the framework of this model, they should have occurred there in the past or may yet remain there undiscovered. If representatives of this group still exist in Africa, then they would probably be restricted to areas of wet rainforest like their American and Asian relatives. With these assumptions of habitat preference, penichrolucanines could be expected to occur only in the forested areas of extreme southern Ivory Coast, Ghana and Nigeria, the Cameroons, and the Congo and Ubangi River drainages. Coincidentally, these areas are similar to Laurent's (1973) postulated refuge areas of African lowland tropical forests.

Conversely, penichrolucanines may be extinct in Africa. Raven and Axelrod (1974) proposed a model reconstructing humid forests covering virtually all of Africa (except the south) until the Neogene (26 MYBP). These forests, extending over what is now the Sahara desert, could have been suitable habitat to ancestral Penichrolucaninae. Raven and Axelrod continue by characterizing the Miocene onward as a time of massive African extinctions resulting from dramatic climatic changes. Eastern Africa was uplifted approximately 2,400 meters since the Miocene, and arid climates have spread over the continent. Also beginning in the Miocene, the Benguela current brought cold water to the west coast of Africa. The changing climate subjected an area covered with rainforest to only seasonal precipitation. Moreover, the trend toward aridity was increased by Pleistocene arid cycles, a phenomenon further reducing the extent of tropical rainforests. Extinctions among the African biota were pronounced during the Neogene and later times, and these authors conclude that it is not surprising that Africa has the most impoverished of all tropical biotas. Livingstone (1982) noted that there has been no period of long stability for African forests.

*Asia.*— The position of Asia *vis-a-vis* Gondwanaland as well as Asian paleoclimates remain largely unknown. There may have been only poor links to Gondwana, but geological and paleontological studies are still inadequate in quality and quantity to position this area unambiguously relative to the other continental blocks (Tarling, 1980). How, then did the Penichrolucaninae get to Asia if they had a Gondwanaland origin? The history of distribution of elephants may help provide the answer.

Africa was variably joined to Europe prior to the early Paleocene, 63 MYBP (Dietz and Holden, 1970; Phillips and Forsyth, 1972; Pitman and Talwani, 1972; Smith, 1971). Dewey *et al.* (1973) suggested that Africa and Europe became more widely separated from the early Paleocene (63 MYBP) to about the upper Eocene (53 MYBP). Berggren and Couvring (1974) indicated that African reconnection with Eurasia may have occurred for a short period in the Eocene-Oligocene (approximately 40-35 MYBP). In any event, a close African-Eurasian connection was established in the middle Miocene about 18 MYBP (Cooke, 1972; Dewey *et al.*,



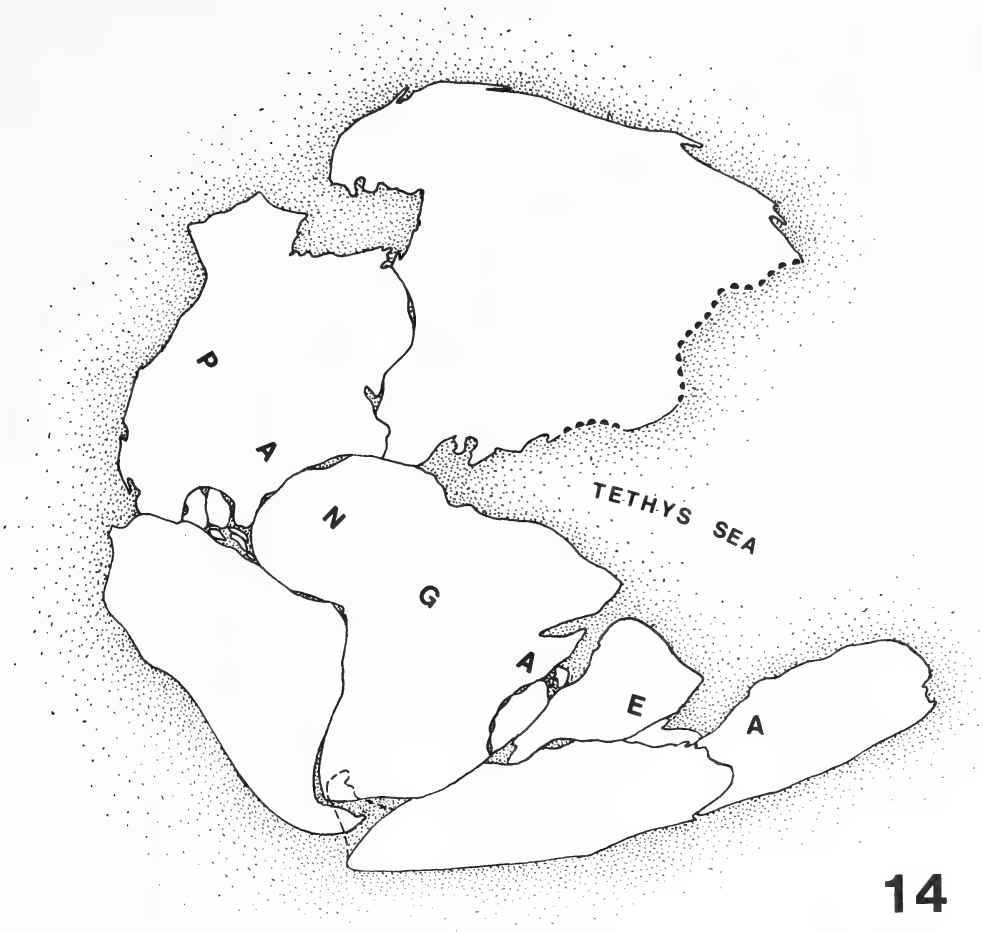


Fig. 14. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Reconstruction of Pangaea at the end of the Permian, 225 MYBP.

1973; Hallam, 1973) that ended Africa's long period of isolation from Eurasia. Eocene mammals of Africa are wholly endemic, but decreasing endemism is exhibited through the Oligocene and Miocene into the Pliocene, with the most frequented (if not the only) migration route being to and from western Asia (Coryndon and Savage, 1973). One of the best known groups, the proboscideans, first migrated to Asia in about early Miocene time; the later Miocene marks the time of strongest links for the whole mammal fauna (Hallam, 1981).

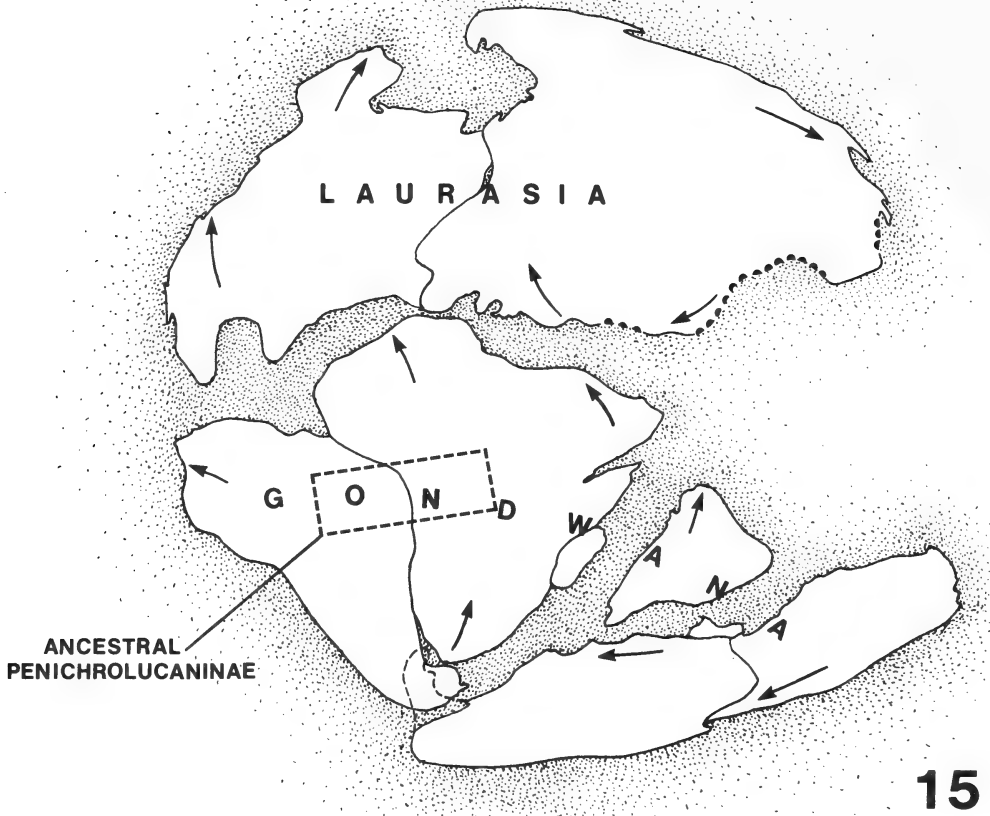


Fig. 15. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Initial rifting of Pangaea as of the end of the Triassic, 180 MYBP with proposed ancestral Penichrolucaninae established in Gondwana. Population boundary is simply to show occurrence on both continents.

This model suggests that the Penichrolucaninae dispersed from Africa to Asia. When they did this is unknown, but the middle Miocene and later is most suitable for this hypothesis for it was during this time period that there began an abundant interchange of organisms, particularly tropical organisms, between Africa and Eurasia. Proboscideans, hippopotamids, and giraffids, for example, dispersed from Africa to Indomalesia. These animals today are primarily savanna dwelling forms, but this is not considered true for their shorter limbed ancestors which occupied forests or gallery woodlands. Raven and Axelrod (1974) report an

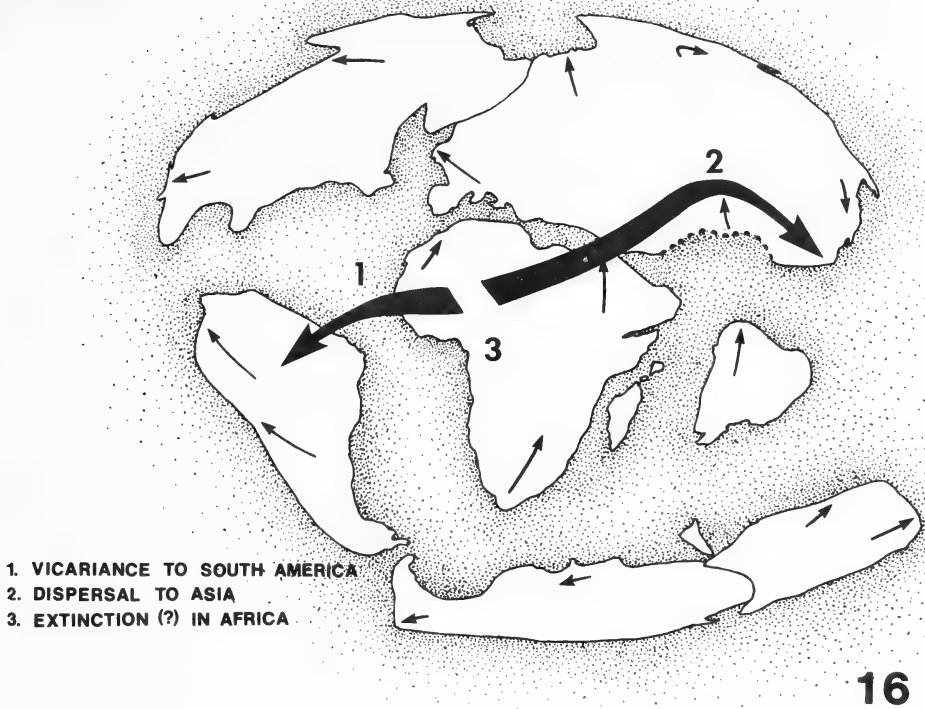


Fig. 16. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Continents as they appeared at the end of the Cretaceous, 65 MYBP and how rifting accounts for present day distribution.

almost complete floristic continuity at family and often generic level between Africa and Southeast Asia that indicates ease of migration between these two areas into early Paleogene time and again in the Neogene when overland connections were restored. Dispersal from the Malayan Peninsula to the islands of the Sunda region and then to the Solomons in the western Pacific would then be the same as already outlined in the first model.

## REJECTED DISPERSAL HYPOTHESES

The preceding two biogeographic interpretations seem most likely to me based on evidence currently available. The following hypotheses are discussed and found unacceptable.

### South American Origin

The data do not support a post-rifted, South American origin for the subfamily. To do so would imply upper Cretaceous dispersal to Antarctica and Australia that would then have taxa raft to Asia when the Australian and Asian plates collided in the Miocene. Although there has been substantial Malaysian biotic introgression to Australia, there has been virtually no movement from Australia to Malaysia (Carne, 1957; Keast, 1972b; Raven and Axelrod, 1974).

Radiation from South America into North America and then to Asia via the Bering Strait is another possibility. This route would require a post-Pliocene movement because it was not until this time that a Panamanian land bridge was established (5.7 MYBP) in Central America to permit dispersal from South America into North America. It is doubtful that a rainforest habitat would have been available to these animals at this time along the entire route. Such a route also implies rapid dispersal over a very long distance.

I believe both of these ideas are untenable in view of what we know of past and present animal dispersal and earth history.

### Indian Rafting

India probably did not serve in the capacity of a Noah's Ark and raft the ancestors of *Penichrolucanus* from a Gondwanan origin to the shores of Asia. India drifted 9,000 km during 200 million years of isolation (Dietz and Holden, 1970) and crossed latitudinal belts of climate which led to widespread impoverishment of its indigenous biota (Raven and Axelrod, 1974). India collided with Asia by the middle Eocene, 45 MYBP (Powell and Conaghan, 1973). Upper Eocene mammal faunas there are distinctly Laurasian in character as is the Recent biota. Floristically, India has few endemics compared to other tropical regions (Raven and Axelrod, 1974). It seems apparent that the long period of Indian drift was characterized by conditions too harsh to permit survival of presumed rainforest inhabiting ancestors of *Penichrolucanus*, even if they did occur in India in the past.

### Summary

- 1a. The Penichrolucaninae originally radiated from holarctic Asia or North America prior to the middle Miocene, approximately 20 MYBP. The subfamily is known from both the Old World and New World tropics implying antiquity for the group.
- 1b. Retreat to the tropical refuges of Indomalesia occurred post-Miocene and to tropical South America post-Pliocene when water barriers were reduced or eliminated and as tropical climates in northern latitudes deteriorated. Both plants and tapirs in the Old and New Worlds demonstrate parallel distributions with the Penichrolucaninae.
- 2a. An alternate hypothesis suggesting a Gondwanan origin and radiation prior to the middle Cretaceous (approximately 110 MYBP) is not ruled out although it seems less likely due to absence of penichrolucanines in Africa.
- 2b. In this second model, occurrence in South America resulted from vicariance between Africa and South America. Representatives of the subfamily remain undiscovered or else are extinct in Africa. If still present in Africa, they would be found in the belt of tropical forests surrounding the Congo and Ubangi Rivers. The ancestors of *Penichrolucanus* dispersed from Africa to Asia, probably during the middle Miocene.
- 3a. Both models converge at this point to suggest dispersal to insular Malaya and Sumatra during periods of glacial maxima in the Pleistocene when sea levels were lowered in this area.
- 3b. The ancestors of *P. leverii* dispersed from a Sunda source to the Solomon Islands probably by sweepstakes dispersal no sooner than the Miocene (time of Solomons formation) and probably not later than the Pleistocene. Long isolation of this taxon is inferred by its retention of primitive character states.

4. The conclusions of the biogeographical analysis (either scenario) support, by congruence, the hypothesis of relationships proposed for the subfamily.

#### ACKNOWLEDGEMENTS

Henry Howden (Carleton University, Ottawa), Antonio Martinez (CNICT, Salta, Argentina), and Francisco Periera (Instituto Biologico, São Paulo, Brazil) all provided helpful comments regarding this study. Michael Bacchus (British Museum of Natural History) loaned me the Arrow types of *Penichrolucanus*. The type of *Brasilucanus alvarengai* was kindly loaned to me by Moaçir Alvarenga (Rio de Janeiro, Brazil); and Quentin Wheeler (Cornell University, Ithaca) and Barry Valentine (Ohio State University, Columbus) loaned additional material under their care. I thank Mark Marcuson for preparing the figures and Gail Littrell for typing the manuscript. An earlier draft of this paper was read by Patricia Freeman, John Lynch, and Michael Voorhies (all University of Nebraska) and Gerald Noonan (Milwaukee Public Museum) who offered valuable suggestions for its improvement. The results of this study do not necessarily reflect the views of these reviewers. I am especially grateful to Michael Voorhies and Gerald Noonan who gave freely of their time to provide extensive critique, clarifications, and alternate ways of considering the biogeographical portion of this study.

#### LITERATURE CITED

- Ab'Sáber, A.N. 1982. The paleoclimate and paleoecology of Brazilian Amazonia. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 41–59. Columbia University Press, New York.
- Arrow, G. 1935. A contribution to the classification of the coleopterous family Lucanidae. *Transactions of the Royal Entomological Society of London* 83: 105–125.
- . 1938. Some notes on stag-beetles (Lucanidae) and description of a few new species. *Annals and Magazine of Natural History (Ser. 11)* 2: 49–63.
- . 1949. *The Fauna of British India Including Pakistan, Ceylon, Burma, and Malaya. Coleoptera, Lamellicornia, Vol. IV. Lucanidae and Passalidae*. Taylor and Francis, Ltd., London.
- Audley-Charles, M.G. and D.A. Hooijer. 1973. Relation of Pleistocene migrations of pygmy stenodonts to island arc tectonics in eastern Indonesia. *Nature* 241: 197–198.
- Ball, I.R. 1975. Nature and formulation of biogeographical hypotheses. *Systematic Zoology* 24: 407–430.
- Beaufort, L.F. de. 1951. *Zoogeography of the Land and Inland Waters*. Macmillan, New York.
- Benesh, B. 1960. *Coleopterorum Catalogus Supplementa*. Lucanidea (sic). W. Junk, Gravenhage.
- Berggren, W.A. and J.A. Van Couvering. 1974. Neogene geochronobioclimatopaleomagnetostatigraphy: a Mediterranean synthesis. Abstracts and Papers, 1974 Annual Meeting of the Geological Society of America, pp. 1022–1024.
- Biswas, B. 1973. Quaternary changes in sea-level in the South China Sea. *Bulletin of the Geological Society of Malaysia* 6: 229–255.
- Brown, K.S., Jr. 1977. Centros de evolução refugias quaternários e conservação de patrimônios

genéticos na região neotropical: padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazonica* 7: 75–137.

- 
- \_\_\_\_\_, P.M. Shepard and J.R.G. Turner. 1974. Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proceedings of the Royal Society of London (B)* 187: 369–378.
- Camp, W.H. 1952. Phytophyletic pattern on lands bordering the South Atlantic basin. *Bulletin of the American Museum of Natural History* 99: 205–212.
- Carne, P.B. 1957. *Systematic Revision of the Australian Dynastinae*. Division of Entomology, CSIRO, Melbourne.
- Colbert, E.H. 1974. *Wandering Lands and Animals*. Hutchinson, London.
- Cooke, H.B.S. 1972. The fossil mammal fauna of Africa. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, pp. 89–139. State University of New York Press, Albany.
- Coryndon, S.C. and R.J.G. Savage. 1973. The origin and affinities of African mammal faunas. In, N.F. Hughes (ed.), *Organisms and Continents Through Time*. Palaeontological Association of London, Special Papers in Palaeontology No. 12: 121–135.
- Cox, B.C. 1974. Vertebrate paleodistributional patterns and continental drift. *Journal of Biogeography* 1: 75–94.
- Darlington, P.J., Jr. 1957. *Zoogeography: The Geographical Distribution of Animals*. John Wiley and Sons, Inc., New York.
- Dewey, J.F., W.C. Pitman III, W.B.F. Ryan and J. Bonin. 1973. Plate tectonics and the evolution of the Alpine system. *Bulletin of the Geological Society of America* 84: 3137–3180.
- Deyrolle, H. 1863. Nouveau genre de lucanide. *Annales de la Société Entomologique de France* 1863: 485–487.
- Didier, R. and E. Séguy. 1953. *Catalogue Illustré des Lucanides du Globe. Texte*. Paul Lechevalier, Paris.
- Dietz, R.S. and J.C. Holden. 1970. Reconstruction of Pangaea; breakup and dispersion of continents, Permian to Present. *Journal of Geophysical Research* 75: 4939–4956.
- Dorf, E. 1957. The Earth's changing climates. *Weatherwise* 10: 54–59.
- Duellman, W.E. 1982. Quaternary climatic-ecological fluctuations in the lowland tropics: frogs and forests. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 389–402. Columbia University Press, New York.
- Endler, J.A. 1982a. Pleistocene forest refuges: fact or fancy? *Ibid*, pp. 641–657.
- \_\_\_\_\_. 1982b. Problems in distinguishing historical from ecological factors in biogeography. *American Zoologist* 22: 441–452.
- Geyh, M.A., H.R. Kudrass and H. Streif. 1979. Sea-level changes during the late Pleistocene and Holocene in the Strait of Malacca. *Nature* 278: 441–443.
- Gose, W.A., G.R. Scott and D.K. Swartz. 1980. The aggregation of Mesoamerica: paleomagnetic evidence. In, R.H. Pilger, Jr. (ed.), *The Origin of the Gulf of Mexico and the Early Opening of the Central North Atlantic Ocean*, p. 51–54. Symposium Proceedings, Louisiana State University and Louisiana Geological Survey, Baton Rouge.
- Hackman, B.D. 1971. The Solomons fractured arc. *Record of Proceedings, Twelfth Pacific Science Congress* 1: 366.
- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131–137.
- \_\_\_\_\_. 1978. Distribution of Amazon forest birds. *Bonner Zoologische Beiträge* 29:

- 38–78.
- \_\_\_\_\_. 1982. General aspects of the refuge theory. In, G.T. Prance (ed.), *Biological diversification in the Tropics*, pp. 6–24. Columbia University Press, New York.
- Hallam, A. 1973. Distributional patterns in contemporary terrestrial and marine animals. In, N.F. Hughes (ed.), *Organisms and Continents Through Time*. Palaeontological Association of London, Special Papers in Palaeontology No. 12: 93–105.
- \_\_\_\_\_. 1981. Relative importance of plate movement, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. In, G. Nelson and D.E. Rosen (eds.), *Vicariance Biogeography. A Critique*, p. 303–330. Columbia University Press, New York.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.
- Hershkovitz, P. 1972. The Recent mammals of the Neotropical Region: a zoogeographic and ecological review. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, pp. 311–431. State University of New York Press, Albany.
- Holloway, B.A. 1960. Taxonomy and phylogeny in the Lucanidae (Insecta: Coleoptera). *Records of the Dominion Museum* 3: 321–365.
- Hooijer, D.A. 1967. Indo-Australian insular elephants. *Genetica* 38: 143–162.
- \_\_\_\_\_. 1975. Quaternary mammals west and east of Wallace's Line. In, G.-J. Barstra and W.A. Casparie (eds.), *Modern Quaternary Research in Southeast Asia*, pp. 37–46. A.A. Balkema, Rotterdam.
- Howden, H.F. 1981. Zoogeography of some Australian Coleoptera as exemplified by the Scarabaeoidea. In, A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 1009–1035. W. Junk, the Hague.
- Johnson, D.L. 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *Journal of Biogeography* 7: 383–398.
- Keast, A. 1972a. Continental drift and the evolution of the biota on southern continents. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, p. 23–87. State University of New York Press, Albany.
- \_\_\_\_\_. 1972b. Australian mammals: zoogeography and evolution. *Ibid*, p. 195–246.
- Kuenen, P.H. 1950. *Marine Geology*. John Wiley & Sons, Inc., New York.
- Laurent, R.F. 1973. A parallel survey of equatorial amphibians and reptiles in Africa and South America. In, B.J. Meggers, E.S. Ayensu and W.D. Duckworth (eds.), *Tropical Forest Ecosystems in Africa and South America: a Comparative Review*, pp. 259–266. Smithsonian Institution Press, Washington, D.C.
- Lavocat, R. 1980. The implications of rodent paleontology and biogeography to the geographical sources and origin of Platyrrhine primates. In, R.L. Ciochon and A.B. Chiarelli (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*, pp. 93–102. Plenum Press, New York.
- Leopold, E.B. and H.D. MacGinitie. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. In, A. Graham (ed.), *Floristics and Paleofloristics of Asia and Eastern North America*, pp. 147–200. Elsevier, New York.
- Livingstone, D.A. 1982. Quaternary geography of Africa and the refuge theory. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 523–536. Columbia University Press, New York.
- Lloyd, J.J. 1963. Tectonic history of the south Central-American orogen. In, O.E. Childs and B.W. Beebe (eds.), *Backbone of the Americas*, pp. 88–100. American Association of

- Petroleum Geologists Memoir No. 2.
- Lynch, J.D. 1982. Relationships of the frogs of the genus *Ceratophrys* (Leptodactylidae) and their bearing on hypotheses of Pleistocene forest refugia in South America and punctuated equilibria. *Systematic Zoology* 31: 166–179.
- MacGinitie, H.D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83: 1–140.
- Medway, L. 1972. The Quaternary mammals of Malesia: a review. *In*, P. and M. Ashton (eds.), *The Quaternary Era in Malesia*, pp. 63–98. Department of Geography, University of Hull, England.
- Meijer, W. 1974. Plant geographic studies on Dipterocarpaceae in Malesia. *Annals of the Missouri Botanical Gardens* 61: 806–818.
- . 1982. Plant refuges in the Indo-Malesian Region. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 576–584. Columbia University Press, New York.
- Moore, B.P. 1978. A new Australian stag beetle (Coleoptera: Lucanidae) with Neotropical affinities. *Journal of the Australian Entomological Society* 17: 99–103.
- Müller, P. 1973. *The Dispersal Centers of Terrestrial Vertebrates in the Neotropical Realm. Biogeographica II*. W. Junk, the Hague.
- Phillips, J.D. and D. Forsyth. 1972. Plate tectonics, paleomagnetism, and the opening of the Atlantic. *Bulletin of the Geological Society of America* 83: 1579–1600.
- Pitman, W.C. III and M. Talwani. 1972. Sea-floor spreading in the North Atlantic. *Bulletin of the Geological Society of America* 83: 619–646.
- Powell, C.M. and P.J. Conaghan. 1973. Plate tectonics and the Himalayas. *Earth and Planetary Science Newsletter* 20: 1–12.
- Prance, G.T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazonica* 3: 5–28.
- . 1982. Forest refuges: evidence from woody angiosperms. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 137–158. Columbia University Press, New York.
- Quantin, P. 1971. On the nature and fertility of volcanic ash soils derived from Recent volcanic eruptions in the New Hebrides Archipelago. *Record of Proceedings, Twelfth Pacific Science Congress* 1: 5–6.
- Radinsky, L. 1963. Origin and early evolution of North American Tapiroidea. *Bulletin of the Peabody Museum of Natural History* 17: 1–106.
- Raven, P.H. and D.I. Axelrod. 1972. Plate tectonics and Australasian paleogeography. *Science* 176: 1379–1386.
- . 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.
- Romer, A.S. 1945. *Vertebrate Paleontology*. University of Chicago Press, Chicago.
- Roon, G. van. 1910. *Coleopterorum Catalogus* 29 (Pars 8. Lucanidae). W. Junk, Berlin.
- Sartono, S. 1973. On Pleistocene migration routes of vertebrate fauna in southeast Asia. *Bulletin of the Geological Society of Malaysia* 6: 273–286.
- Schultz, C.B., L.D. Martin and R.G. Corner. 1975. Middle and Late Cenozoic tapirs from Nebraska. *Bulletin of the University of Nebraska State Museum* 10: 1–21.
- Schuster, R.M. 1972. Continental movements, "Wallace's line" and Indomalayan-Australasian



- dispersal of land plants: some eclectic concepts. *Botanical Review* 38: 38–86.
- Seyfert, C.K. and L.A. Sirkin. 1973. *Earth History and Plate Tectonics*. Harper and Row, New York.
- Simpson, B.B. and J. Haffer. 1978. Speciation patterns in the Amazonian forest biota. *Annual Review of Ecology and Systematics* 9: 497–518.
- Smith, A.G. 1971. Alpine deformation and the oceanic areas of the Tethys, Mediterranean, and Atlantic. *Bulletin of the Geological Society of America* 82: 2039–2070.
- Smith, A.G. and J.C. Briden. 1977. *Mesozoic and Cenozoic Palecontinental Maps*. Cambridge University Press, Cambridge.
- Tarling, D.H. 1971. Gondwanaland, paleomagnetism and continental drift. *Nature* 229: 17–21, 71.
- . 1980. Continental drift and biological evolution. *Carolina Biology Readers* 113: 1–32.
- Tricart, J. 1974. Existence de périodes sèches au Quaternaire en Amazonie et dans les régions voisines. *Revue de Géomorphologie Dynamique* 4: 145–158.
- Umbgrove, J.H.F. 1938. Geological history of the East Indies. *Bulletin of the American Association of Petroleum Geologists* 22: 1–70.
- Veevers, J.J., G. Jones and J.A. Talent. 1971. Indo-Australian stratigraphy and the configuration and dispersal of Gondwanaland. *Nature* 229: 383–388.
- Verstappen, H.Y. 1975. On palaeoclimates and landform development in Malesia. In, G.-J. Barstra and W.A. Casparie (eds.), *Modern Quaternary Research in Southeast Asia*, pp. 3–35. A.A. Balkema, Rotterdam.
- Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* 173: 771–780.
- Vulcano, M.A. and F.S. Pereira. 1961. A subfamília Penichrolucaninae representada em América (Col., Lucanidae). *Studia Entomologica* 4: 471–480.
- Walker, D. 1982. Speculations on the origin and evolution of Sunda-Sahul rain forests. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, p. 554–575. Columbia University Press, New York.
- Watrous, L.E. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30: 1–11.
- Woodring, W.P. 1954. Caribbean land and sea through the ages. *Bulletin of the Geological Society of America* 65: 719–732.



## TSETSE GENETICS: A REVIEW

R. H. Gooding  
Department of Entomology  
University of Alberta  
Edmonton, Canada, T6G 2E3

*Quaestiones Entomologicae*  
20: 89-128 1984

### ABSTRACT

*About 140 papers were reviewed and the following aspects of tsetse genetics discussed: cytogenetics, sex determination, visible traits, biochemical and molecular genetics, vectoring ability, behavioural genetics, linkage groups, population genetics, genetic aspects of radiation and chemosterilants, and genetic aspects of reproductive strategies (such as multiple matings, sperm precedence, interspecific mating and hybridization). Genetic information is most extensive for *Glossina morsitans morsitans* Westwood and substantial amounts of information exist for other members of the *morsitans* group and for members of the *palpalis* group. Information on genetics of members of the *fuscus* group is restricted to cytological observations on two species. Of three species groups recognized on the basis of structural and ecological features, two are supported by available genetic information. Genetic data are insufficient to determine if the *fuscus* group can be defined on the basis of such features.*

### RÉSUMÉ

*L'auteur passe en revue environ 140 articles donnant des informations sur la génétique des mouches tsé-tsé et discute des aspects suivants: la cytogénétique, la détermination du sexe, les traits visibles, la génétique moléculaire et biochimique, la capacité vectorielle, la génétique du comportement, les groupes de liaison, la génétique des populations, les aspects génétiques de l'irradiation et des chimiostérilisants, et les aspects génétiques des stratégies reproductrices (comme l'accouplement multiple, la préséance du sperme, l'accouplement interspécifique et l'hybridation). *Glossina morsitans morsitans* est l'espèce dont la génétique est la mieux connue, mais il existe aussi des informations substantielles concernant les autres membres du groupe *morsitans* et ceux du groupe *palpalis*. Concernant le groupe *fuscus*, il n'existe que quelques observations cytologiques sur deux espèces. Les données génétiques disponibles supportent l'établissement de deux des trois groupes d'espèces définis à partir de traits morphologiques et écologiques. Les données sont insuffisantes pour établir si le groupe *fuscus* peut aussi être défini à partir de tels traits génétiques.*

### Table of Contents

Introduction .....	90
Cytogenetics .....	90
Sex Determination .....	95
Visible Traits .....	96
Biochemical and Molecular Genetics .....	98
Vectoring Ability .....	102
Behavioural Genetics .....	103
Linkage Groups .....	104
Population Genetics .....	105
Genetic Aspects of Radiation and Chemosterilants .....	110
Some Genetic Aspects of Reproduction .....	115

Concluding Remarks ..... 119

References ..... 120

INTRODUCTION

There are about 30 species and subspecies of tsetse flies (Jordan 1977; Potts 1973), all of which belong to the genus *Glossina* Wiedemann. Within the genus species are placed in three species groups or subgenera (Newstead *et al.* 1924; Glasgow 1970; Potts 1973; Jordan 1977): subgenus *Austenina* Townsend = *fusca* group (14 taxa); subgenus *Nemorhina* Robineau-Desvoidy = *palpalis* group (9 taxa); subgenus *Glossina* s. str. = *morsitans* group (7 taxa). These divisions are based largely upon structure.

Males and females of all tsetse species are haematophagous and feed fairly often. Females of most species mate when fairly young and apparently can store viable sperm for the rest of their lives. A single egg is matured at a time and fertilization is internal. At the end of embryogenesis the first instar larva hatches and it and the subsequent two instars are nourished by secretions from the "milk glands" of the female. When a female is approximately 16 days old she deposits her first offspring. Ovulation takes place shortly after larviposition and females are able to produce a larva about every nine days. Although females are long lived, only a modest number of offspring (probably no more than 6 or 8 in a well managed colony and considerably fewer under field conditions) are produced per female. Tsetse flies contain symbiotic bacteroids in a mycetome located in the anterior part of the midgut, as well as rickettsia-like organisms demonstrable in the nurse cells and developing oocyte. These symbionts undoubtedly play a role in the reproduction of the fly and may have the potential to influence the inheritance of certain traits. (For recent reviews of tsetse physiology see Langley (1977) and Tobe and Langley (1978).)

Tsetse flies are confined to Africa between 5°N latitude and 20°S latitude (Potts 1973) and their importance as vectors of African trypanosomiasis is well known. Largely because of their vectoring capacity, tsetse flies have been intensively studied and there exists a large body of information on their biology, physiology, ecology and medical/veterinary importance. However, for a variety of reasons (including their low rate of reproduction, and until fairly recently, difficulties in maintaining colonies), comparatively little work has been done on their genetics. For example, as late as 1963 intra-taxon variations known to occur in nature were all attributed, in whole or in large part, to environmental effects (Glasgow 1963).

With the current interest in non-chemical control of pests, the situation has been redressed somewhat, and research on tsetse genetics is proceeding in several laboratories. I therefore feel that this is an opportune moment to summarize the literature on tsetse genetics, to evaluate its contribution to our understanding of these flies, and to indicate areas where further work is needed.

CYTOGENETICS

Cytogenetic studies of tsetse flies began with the (unpublished) demonstration by Slizynski (cited by Vanderplank 1948) that *G. m. centralis* has 3 pairs of chromosomes. Since then karyotypes have been determined for about half the taxa, meiosis has been described in detail for both males and females of several taxa, and detailed comparisons of some taxa using Giemsa C-banding and polytene chromosomes have been carried out. In the present section I

Table 1. Chromosome formulae for *Glossina* species.

Species	Formula <sup>1</sup> ( $2n =$ ) <sup>2</sup>	Refs. <sup>3</sup>
Group I		
<i>fusca congolensis</i> Newstead & Evans	$18L + 2M_{10} + (XX/XY)$	A B C
<i>brevipalpis</i> Newstead	16	D
Group II		
<i>palpalis palpalis</i> (Robineau-Desvoidy)	$2L_1 + 2L_2 + (XX/XY)$	E F G H
<i>palpalis gambiensis</i> Vanderplank	$2L_1 + 2L_2 + (XX/XY)$	H I
<i>tachinoides</i> Westwood	$2L_1 + 2L_2 + (XX/XY)$	B H J K L
<i>fuscipes fuscipes</i> Newstead	$2L_1 + 2L_2 + (XX/XY)$	B D H K L M N
Group III		
<i>longipalpis</i> Wiedemann	$4L + 2M + 2Sh (= 2S?)$	E
<i>morsitans morsitans</i> Westwood	$2L_1 + 2L_2 + (XX/XY) + 2-7S$	B H J K L O P Q R
<i>morsitans submorsitans</i> Newstead	$2L_1 + 2L_2 + (XX/XY) + 2-7S$	H Q
<i>morsitans centralis</i> Machado	$2L_1 + 2L_2 + (XX/XY) + 1-3S$	D H Q
<i>pallidipes</i> Austen	$2L_1 + 2L_2 + (XX/XY) + 0-2S$	D H O S T
<i>austeni</i> Newstead	$2L_1 + 2L_2 + (XX/XY) + 8-12S$	B K L O P
<i>swynnertoni</i> Austen	8	D H Q U

<sup>1</sup> As far as possible the most recent terminology is used: A=autosome; L, L<sub>1</sub>, L<sub>2</sub>=long autosomes; M=medium autosome; Sh=short autosome; S=supernumerary or B chromosomes.

<sup>2</sup> Aneuploidy and polymorphisms are discussed in text sections on sex determination and on population genetics.

<sup>3</sup> References: A=Itard 1971b; B=Itard 1973b; C=Itard 1971c; D=Maudlin 1970; E=Baldry 1970; F=Maudlin 1979; G=Riordan 1968; H=Southern 1980; I=Itard 1974; J=Itard 1966; K=Itard 1970a; L=Itard 1971a; M=Maudlin 1968; N=Pell and Southern 1976; O=Amos and Dover 1981; P=Craig-Cameron *et al.* 1973b; Q=Pell *et al.* 1973; R=Southern *et al.* 1972b; S=Hulley 1968; T=Southern and Pell 1981; U=Southern *et al.* 1972a.

shall summarize much of this information but the reader is referred, for additional details, to two other reviews of cytogenetics (Itard 1973b; Southern 1980).

### Chromosome number

Of the 30 taxa in the genus *Glossina*, chromosome formulae have been determined for 13 (two from the *fuscus* group, four from the *palpalis* group, and seven from the *morsitans* group). This subject has been reviewed twice (Itard 1973b; Southern 1980) but is presented here briefly (Table 1) for the sake of completeness. Where sex chromosomes have been identified, females are homogametic (XX) and males are heterogametic (XY). Members of the *fuscus* group have the largest number of chromosomes. The simplest chromosome formula ( $2n = 4$  autosomes + [XX or XY]) occurs among members of the *palpalis* group. Flies of the *morsitans* group are characterized by having, in addition to the basic complement of chromosomes found in the *palpalis* group, a variable number of small, univalent supernumerary (=B) chromosomes which lack (at least during male meiosis) pairing mates. Although there is an obvious need to obtain additional information on the chromosome number in more taxa (notably those of the *fuscus* group), the pattern, with regard to chromosome numbers, which has thus far emerged is consistent with the generally accepted arrangement of the species.

### Chromosome structure

In *G. f. fuscipes* the sex chromosomes and four other pairs are metacentric while six pairs are acrocentric (Itard 1971c). Within the *palpalis* and *morsitans* groups three of the chromosomes are similar in form. The longest chromosome,  $L_1$ , is always submetacentric and has a secondary constriction (the nucleolar organizer region) on the long arm (Southern *et al.* 1972a; Southern and Pell 1973; Itard 1973b; Pell *et al.* 1973).  $L_2$  and X are metacentric (or nearly so) and, except for the X of *G. pallidipes* which has a prominent secondary constriction (Southern and Pell 1981), these chromosomes lack secondary constrictions (Southern *et al.* 1972a; Southern and Pell 1973; Itard 1973b; Pell *et al.* 1973). The heterochromatic Y chromosome is acrocentric in *G. f. fuscipes* and *G. m. morsitans* (Itard 1973b; Pell *et al.* 1973), submetacentric in *G. austeni*, *G. m. submorsitans*, and *G. pallidipes* (Itard 1973b; Pell *et al.* 1973; Southern and Pell 1981) and metacentric in *G. tachinoides*, *G. p. palpalis* and *G. m. centralis* (Itard 1970a, 1973b, 1974; Southern and Pell 1973). Polymorphisms have been observed and are discussed in the section on population genetics. The supernumerary chromosomes are heterochromatic and very short in *G. pallidipes* and *G. m. submorsitans*, longer (and of variable length) in *G. m. morsitans* and *G. austeni*. The supernumeraries of *G. m. centralis* differ from all the others by being metacentric and (as pointed out by Southern 1980) it is interesting to note that the length of each arm is approximately the same as the lengths of the supernumerary chromosomes of *G. pallidipes* and *G. m. submorsitans*. However this may not indicate an evolutionary connection between B chromosomes since studies of satellite DNA indicate that B chromosomes arose from A chromosomes within each taxon (Amos and Dover 1981; see section on biochemical and molecular genetics.)

### Giemsa C-banding patterns

Giemsa C-banding of the  $L_1$ ,  $L_2$ , and X chromosomes conforms to a basic pattern (found in *G. austeni*) with variations occurring mainly among members of the *morsitans* group. Chromosomes in members of the *palpalis* group are remarkably similar to the corresponding

chromosomes in *G. austeni* (Davies and Southern 1976). *G. tachinoides* is unusual in that the banding pattern of the X chromosome is identical to that of chromosome  $L_1$  and that both are remarkably similar to  $L_1$  from *G. p. gambiensis* and *G. p. palpalis* (from Zaire) (Southern 1980). The  $L_2$  and X chromosomes from *G. f. fuscipes* are nearly identical to their homologs in *G. p. palpalis* (from Nigeria) (Southern 1980). These similarities and the amount of intra-taxon variation were used by Southern (1980) to indicate the limited usefulness of the Giemsa C-banding technique for phylogenetic studies. The Y chromosome of *G. m. morsitans* and *G. tachinoides* is uniformly stained, in *G. austeni* it shows a banding pattern, and in *G. f. fuscipes*, *G. p. gambiensis*, and *G. p. palpalis* the Y chromosomes have only one band, uniquely positioned in each species. Supernumeraries found in the *morsitans* group have a Giemsa C-banding pattern similar to the Y chromosome in each taxon (Davies and Southern 1976). More recent work has shown a significant amount of polymorphism in the Giemsa C-banding patterns (Jordan *et al.* 1977; Southern 1980; Southern and Pell 1981) and has revealed that *G. m. centralis* and *G. m. submorsitans* have small non-staining zones in the Y chromosome while in *G. pallidipes* one arm of the Y does not stain (Southern and Pell 1981).

### Polytene chromosomes

Polytene chromosomes have been reported in a number of tissues in larvae, "pupae", and pharate adults within the puparia of several species (Burchard and Baldry 1970; Riordan 1970; Southern *et al.* 1973a, 1973c; Southern and Pell 1973, 1974, 1981; Pell and Southern 1976). The most detailed studies have been by Southern and his colleagues who published photos, diagrams and verbal descriptions of polytene chromosomes found in the trichogen and tormogen cells associated with the macrochaetae on the thoraces of *G. m. morsitans* (Southern *et al.* 1973a, 1973c), *G. austeni* (Southern and Pell 1974), *G. f. fuscipes* (Pell and Southern 1976) and *G. pallidipes* (Southern and Pell 1981). Polytenes have also been studied in other taxa and in some hybrids (Southern and Pell 1973; Pell and Southern 1976) but detailed accounts have not yet been published.

In tsetse flies only  $L_1$ ,  $L_2$ , and X chromosomes form polytenes. Polytene nuclei in trichogen and tormogen cells lack all traces of Y and supernumerary chromosomes, and also lack chromocentres. In describing the polytene chromosomes Southern and his colleagues have divided the six polytene arms in each species into a total of 100 units, each of which was subdivided into two or three divisions. The nucleolar organizer is found at approximately the same location (position 51B to 53B) in  $L_1R$  in each of the species. The region of the X chromosome which associates with the Y chromosome during meiosis is represented by a fibrillar mass.

In these studies *G. austeni* was chosen as a reference species and the percentages of the bands in each species which are represented in *G. austeni* were calculated. Of the three species compared to *G. austeni*, *G. m. morsitans* was the most similar, having from 47.5% (for XL) to 100% (for  $L_1L$ ) of its bands represented in *G. austeni* (Southern and Pell 1974). The corresponding figures for *G. pallidipes* are 23.7% (for XL) and 66.4% (for  $L_1L$ ) (Southern and Pell 1981) and the figures for *G. f. fuscipes* are 12.9% (for XL) and 69.4% (for  $L_1L$ ) (Pell and Southern 1976). The data indicate that chromosome  $L_1$  has undergone the fewest evolutionary changes, and the X chromosome the greatest number of changes. The results also present limited support for placing *G. austeni* in the *morsitans* group rather than in the *palpalis* group but polytene analyses of more taxa are needed, as are detailed comparisons between each of the possible pairs of taxa, before a firm conclusion can be drawn from polytene chromosome data.

### Supernumerary or B chromosomes

The small (usually telocentric) chromosomes found in members of the *morsitans* group were first recognized to be supernumerary or B chromosomes by Itard (1970a). They do not occur in members of the *palpalis* group and too few members of the *fusca* group have been examined to warrant comment on their distribution in that group. The number of supernumeraries varies from individual to individual and, although their numbers usually vary within fixed limits, some populations appear to lack them (Southern 1980). Southern (1980) pointed out that most studies have been done on flies from established colonies and that few localities were sampled to establish these colonies, thus the full extent of variation in the numbers of supernumeraries may not yet be realized. He also pointed out that the consistently pycnotic appearance of the supernumeraries indicates that they are not the site for RNA production but these cytogenetic studies have been done on flies maintained under fairly uniform laboratory conditions and it is possible that supernumeraries have an important role under certain conditions encountered in the field. In support of this Southern (1980) points out that "there is some evidence the individuals of *G. m. morsitans* with six or seven supernumeraries emerge as adults significantly later than those with just two or three."

An analogous situation occurs with Y chromosomes in *G. p. palpalis* (Southern 1980; see also section on sex determination.). Since *G. p. palpalis* lack supernumeraries I wonder if these apparently unrelated situations may not have a similar selective value under natural conditions. There is as yet no satisfactory explanation for the sex chromosome polymorphism observed in natural populations of members of the *palpalis* group (Maudlin 1979). The suggestion (Davies and Southern 1976; Amos and Dover 1981) that the supernumerary chromosomes may have arisen from the Y chromosome may be pertinent to the above. The association of Y chromosomes with the supernumeraries during meiosis in *G. austeni* (Southern and Pell 1973) and the similar Giemsa C-banding patterns of Y chromosomes and supernumerary chromosomes (discussed above) are also consistent with the suggestion that the B chromosomes arose from the Y chromosomes. However the demonstration that Y and B chromosomes do not have extensive satellite DNA similarity (Amos and Dover 1981) does not support the suggestion of an evolutionary relationship between Y and B chromosomes and required a two step hypothesis to explain the evolution of the supernumeraries from the A (probably Y) chromosomes (Amos and Dover 1981).

### Meiosis

Meiosis in tsetse flies has been summarized by Southern (1980) and the reader should consult that review for details. However several aspects of meiosis which pertain to other aspects of tsetse genetics covered in this review will be discussed briefly here.

Spermatocyte nuclei in *G. austeni* contain a large vesicle containing extra-chromosomal DNA (Southern and Pell 1973) which is apparently responsible for synthesis of an RNA which remains within the nucleus and is ultimately reorganized into fibres (Craig-Cameron *et al.* 1974). The vesicle is absent from *G. m. submorsitans* and *G. m. centralis* (Southern and Pell 1973). A small vesicle was found in *G. m. morsitans* recently isolated from Africa and from a colony maintained at Langford England, but it suddenly disappeared from the latter suggesting some environmental influence upon its expression (Southern and Pell 1973; Craig-Cameron *et al.* 1974).

In the *morsitans* group, pairing between the X and Y chromosomes during meiosis always involves a segment of the X chromosome adjacent to the centromere but the segment of the Y



chromosome involved in the pairing varies from species to species (Southern *et al.* 1972a, 1972b; Southern and Pell 1973; Southern 1980). Since pairing between X and Y chromosomes of *G. pallidipes* apparently does not occur (Southern 1980; Southern and Pell 1981) it is possible that the pairing segment is missing from one of the chromosomes (probably the Y chromosome). Pairing between the X and Y chromosomes of *G. m. morsitans* involves two heterochromatic segments and is achiasmatic (Southern *et al.* 1972b; Southern and Pell 1973).

Meiosis in male and female tsetse flies differs with regard to three phenomena: formation of chiasmata, behaviour of the B chromosomes, and timing. Chiasmata are found during female meiosis (Davies and Southern 1977) and only rarely during male meiosis in *G. m. morsitans* (Craig-Cameron *et al.* 1973a, 1973b; Southern and Pell 1973; Southern 1980) suggesting that genetical recombination is more frequent in females than in males. (See section on linkage groups.) Chiasmata occur during female meiosis (Davies and Southern 1977) but not during male meiosis in *G. austeni* (Craig-Cameron *et al.* 1973a, 1973b). Chiasmata were reported in about 1% of male *G. f. fuscipes* and such males often showed "at least three apparent chiasmata per nucleus in L<sub>1</sub> and L<sub>2</sub> bivalents" (Pell and Southern 1976). Perhaps there is a locus controlling genetical recombination in tsetse flies with the population of *G. f. fuscipes* examined having a rare allele which permits the process in males. During male meiosis the supernumerary (or B) chromosomes behave as univalents and are distributed randomly to the poles while in females they appear to form true bivalents which segregate at anaphase I (Davies and Southern 1977). Male meiosis is completed within a few hours nine to ten days after larviposition (Southern *et al.* 1972b) while in females meiosis occurs throughout adult life and metaphase I of meiosis may last from a few hours (during the first reproductive cycle) to six or seven days (during subsequent cycles) (Davies and Southern 1977).

Meiosis in *morsitans* group hybrid males proceeds normally (Southern and Pell 1973; Southern *et al.* 1973b), but in hybrid males in the *palpalis* group the chromosomes tend to fragment during meiosis (Southern 1980). (This latter observation does not seem consistent with Vanderplank's (1948) observation that hybrid males in the *palpalis* group are fertile if they can successfully transfer sperm. See section on paternal aspects of hybridization.) In both groups hybrid females are (to varying degrees) fertile. The above observations, combined with the extensively similar polytene banding patterns observed in closely related taxa, suggests not only that genetic material may be passed from one taxon to another, but that genetical recombination might produce completely new chromosomes and thus novel combinations in the descendants of the hybrids. However, in the only experiment designed to search for genetical recombination in female hybrids (produced by crossing *G. m. morsitans* x *G. m. centralis*), no recombination was found between two X chromosome loci (*ocra* and *salmon*) which, in *G. m. morsitans*, are separated by about 37 map units (Gooding 1982b).

## SEX DETERMINATION

In all tsetse species studied which have sex chromosomes, males are heterogametic (i.e. males are XY and females are XX). Aneuploidy involving the Y chromosome is wide-spread among tsetse species (Southern 1980) but sex chromosome aneuploidism is most easily studied, and has been most extensively studied, in members of the *palpalis* group since these flies lack supernumerary chromosomes. Sex chromosome aneuploidy occurs in both field populations (Maudlin 1979) and laboratory colonies (Southern 1980) of *G. p. palpalis*. The number of Y chromosomes has no effect upon the sex phenotype of the fly (Maudlin 1979; Southern 1980)

and it appears that sex phenotype is determined by a balance between the number of autosomes and the number of X chromosomes: females may be XX, XXY or XXXY; males may be XY, XYY or XO (Maudlin 1979; Southern 1980). The finding that the Y chromosome does not influence the apparent sex of the adult is consistent with an earlier observation in which a mutant *G. m. morsitans* created by  $\gamma$ -irradiation, had a portion of the Y chromosome inserted into one autosome, and had lost at least two-thirds of the long arm of the Y chromosome, yet the males appeared normal (Southern and Pell 1973). The Y chromosome is required for production of motile sperm (Southern 1980) and there is a curious correlation between the number of Y chromosomes in *G. p. palpalis* and the time spent in the puparium. Those flies lacking a Y chromosome (XX or XO) emerge 24-36 hours before flies having one Y chromosome (XXY or XY); and those with two or three Y chromosomes (XXYY, XYY, or XXXYY) do not emerge for another 12 hours.

Further evidence to support the hypothesis that sex phenotype is determined by the balance between autosomes and number of X chromosomes could be found by searching for gynandromorphs or for mosaics having male and female characters. The apical bristles on the scutellum in some species show a marked sexual dimorphism (see Buxton 1955, pp. 6-7). Female *G. m. morsitans* have bristles which are much shorter than those of males and we have observed a female having one long and one short bristle. This mosaic is consistent with the hypothesized mechanism for determining sex phenotype but the situation may be more complicated since in one line of *G. m. morsitans* the length of the scutellar apical bristles in females is much longer than normal (unpublished work in my laboratory).

Maudlin (1979) has pointed out that sex ratio distorting genes may exist in tsetse, and in fact significant sex ratio distortion is a feature of the two *G. m. submorsitans* colonies (one from Upper Volta and one from Nigeria) which I maintain in my laboratory. In both colonies there is a significant excess of females and this excess has remained relatively stable over several years and therefore can not be due simply to lethal recessives on the X chromosome. No explanation of this permanent excess of females is yet available.

### VISIBLE TRAITS

Most taxonomic and zoogeographic papers on tsetse refer to variations in structure or colouration of adults, but the extent to which these are under genetic control has not been determined. Despite the large numbers of flies observed during field and laboratory studies each year, few reports have been published describing distinctive intra-population variations in structure or colour. Variations have been found in the colour of *G. m. morsitans* (Shircore 1913) and of *G. brevipalpis* (Burt 1944) but no attempt was made to establish their genetic basis. A brief list of naturally occurring colour variants is provided by Vanderplank (1948) who pointed out that these variants are of no taxonomic significance but may be useful in studying the genetics of body colouration. More recently, mutations controlling body colour (Bolland *et al.* 1974; Vloedt 1980) and eye colour (Gooding 1979) have been found in *G. m. morsitans*, and the genetics of these traits has been described.

*G. m. morsitans* adults have dark brown bodies with brownish-black transverse bands on abdominal tergites and similarly coloured spots on the nota. Two mutant strains having yellowish bodies and yellowish-brown bands or spots have been established. The first, (designated *ocra* = *oc*) was found in a laboratory colony which descended from flies collected near Kariba, Zimbabwe (Bolland *et al.* 1974); the second (designated *oT*) descended from a

male collected near Tanga, Tanzania (Vloedt 1980). The locus for *oc* and *oT* is on the differential part of the X chromosome (Bolland *et al.* 1974; Vloedt 1980; see also section on linkage groups), and these alleles are completely recessive to the wild type allele. Since reciprocal crosses involving females homozygous for either *oc* or *oT*, with males having the other allele, produced offspring having ocra bodies (Vloedt 1980), both alleles must involve the same biochemical or physiological processes. Wild type and ocra males are equally competitive in mating experiments conducted under laboratory conditions (Kawooya 1977; Vloedt 1980). Some females with ocra bodies will mate more than once and, although some females use sperm from two matings, or only from the second mating, most females use only sperm from the first mating. The latter two phenomena are not unique to either *ocra* (studies by Kawooya 1977; Vloedt 1980) or *oT* (studies by Vloedt 1980) (see sections on multiple mating by females and use of sperm by multiply mated females). With respect to most criteria used to measure success of a tsetse colony, *oc* and *oT* were as good as, or better than, wild type flies from Tanzania, although about 10% of the ocra flies tend to lose their wings (Vloedt 1980; Langley, commenting on Vloedt's paper, gave this figure as 30% for his *ocra* colony). However, the success of the ocra flies, under laboratory conditions, is not translated into success in the field. Recapture rate of laboratory reared ocra flies in Tanzania was less than 20% of that of laboratory reared wild type flies (Dame in discussion of Vloedt 1980), indicating fairly strong selection against this phenotype in the field.

Compound eyes of wild type *G. m. morsitans* are dark brown and only one variant (designated *salmon* = *sal* because of the eye colour) has been found (Gooding 1979). The allele *sal* has an X chromosome locus and, at least as regards eye colour, it is completely recessive to the wild type allele (Gooding 1978, 1979). This allele is pleiotropic, affecting a variety of morphological and physiological traits in hemizygous males, and in females homozygous for *sal*: compound eyes and ocelli are salmon and testes are very pale, but the spermathecae are normal (Gooding 1979); heads of salmon flies have less xanthommatin than do those of wild type flies, and salmon flies excrete tryptophan while wild type flies excrete kynurenine (Gooding and Rolseth 1984); adult longevity is shorter, fewer offspring are produced, there is a lower pregnancy rate in females, and mating competitiveness of males is about half that of wild type males (Gooding 1982a); light is detected at a lower intensity, and light adaptation is faster, and occurs at lower light intensity (Davis and Gooding 1983). Although salmon and wild type males differ neither in timing of their spontaneous activities, nor in total number of activity periods, salmon males become active slightly sooner after "lights on", have activity periods of shorter duration and are more responsive to moving images (Gooding 1983b). Unlike the situation with *ocra*, there is evidence for assortative mating (Gooding 1982a; see section on behavioural genetics). Susceptibility to infection with *Trypanosoma brucei brucei* Plummer and Bradford (M'Pondi *et al.*, *in prep.*) and *Trypanosoma congolense* Broden (Distelmans *et al.*, *in prep.*) is greater in salmon males than in wild type males. The biochemical lesion caused by the allele *salmon* is a lack of tryptophan oxygenase activity and this accounts for much of the pleiotropic nature of this allele (Gooding and Rolseth 1984).

Most of the impetus for studying *salmon* comes from the lethal or semi-lethal nature of this maternally influenced, genetically rescuable allele. When *sal/sal* females are mated with hemizygous *sal* males, about 80% of the offspring produced die in the puparia, while adults which do emerge have very pale eyes, and most die within a few days (Gooding 1978, 1979). When *sal/sal* females are mated with wild type males they produce the expected number of

phenotypically wild type females and these have normal viability, but the pale eyed male offspring die, either in the puparia or as young adults (Gooding 1978, 1979). Lethality of *salmon* has been demonstrated at 23°C and 25°C, and in two genetic backgrounds (Gooding 1982a). The possibility of using *salmon* as a genetic control agent has been investigated both theoretically (Gooding 1978, and with an unpublished model which includes provision for density dependent effects) and in experimental laboratory populations (Gooding 1982a). Computer models and laboratory experiments indicate *salmon* may be effective as a genetic control agent if salmon flies behave the same as wild type flies in the field. However, the greater susceptibility of salmon flies to at least two species of trypanosomes makes it unlikely that releases of this fly, into any locality where trypanosomiasis is endemic, could be justified.

Size of tsetse flies may also be considered as a "visible trait". No genetic studies on size *per se* have been undertaken, but heritability ( $h^2$ ) of teneral adult weight has been estimated to be between 0.09 and 0.16 in *G. m. morsitans* (Gooding and Hollebhone 1976). The selective pressures for maintaining fly size within fairly narrow limits in each species have not been determined but extremes of size tend to be eliminated from tsetse populations in nature (Glasgow 1963; Phelps and Clarke 1974).

### BIOCHEMICAL AND MOLECULAR GENETICS

Our knowledge of biochemical genetics of tsetse consists mainly of information on the electrophoretic mobility and banding patterns of several enzymes from whole flies examined on starch gel (Geest and Kawooya 1975; Geest *et al.* 1978; Etten 1982c) or from thoraces, midguts, or testes examined on polyacrylamide gel (Rolseth and Gooding 1978; Gooding and Rolseth 1978, 1979, 1982; Gooding 1981a, 1982b). It is important to realize that not all variation in electrophoretic mobility is due to genetic factors, thus variation in mobility is not proof of genetic variation. For some enzymes the variation in mobility has been shown, by breeding experiments, to be under genetic control; for others the only evidence is that the banding patterns correspond to patterns known to be under genetic control in other species, or the data are consistent with what one would find in a population in Hardy-Weinberg equilibrium.

On starch gel electrophoresis, the following enzymes are monomorphic (i.e. only one allele has been demonstrated) in laboratory colonies of *G. m. morsitans*. The designation of the locus is given, in italics: lactic dehydrogenase (*ldh*), malic dehydrogenase (*mdh*, Geest and Kawooya 1975; but see also Table 2); NADP-dependent malic dehydrogenase (*mdh-t*, Geest and Kawooya 1975; but information on this enzyme was later withdrawn by Geest *et al.* 1978 as being "in error".); an esterase (*est*, Geest *et al.* 1978; see also Table 2); adenylate kinase (*Ak*), catalase (*Cat*), isocitrate dehydrogenase (*Idh*), phosphoglucosomerase (*Pgi*), peroxidase (*Po*, Geest *et al.* 1978); glucose-6-phosphate dehydrogenase (*G-6-pd*, Geest *et al.* 1978; but see also Table 2). Variation in mobility of xanthine dehydrogenase (*Xdh*) was believed by Geest and Kawooya (1975) to be due to non-genetic factors.

Variations seen in electrophoretic banding patterns of alkaline phosphatase (*alph*) and a leucine aminopeptidase (*lap*<sub>2</sub>) in *G. m. morsitans* (Geest and Kawooya 1975) may or may not be under genetic control. For alkaline phosphatase there were 140 flies with a double band pattern and two flies which had an additional double band, and for leucine aminopeptidase all 480 flies had a double banded pattern but for one fly the migration of these bands was less than in the other flies. No genetic model was offered for either *alph* or *lap*<sub>2</sub> and the frequency of the

Table 2. Genetics of molecular variation in *G. m. morsitans*.

ENZYMES	LOCUS	NO. ALLELES	HETERO. BANDING <sup>1</sup>	EVID. <sup>2</sup>	REF <sup>3</sup>
aldehyde oxidase	<i>Ao</i> <sup>4</sup>	3	2	2 <sup>5</sup>	A
aldehyde oxidase	<i>Ao</i> <sup>4</sup>	3	3	2,3	B
alkaline phosphatase	<i>Alkph</i>	2	2	2,3	C
arginine phosphokinase	<i>Apk</i>	2	2	2,3	C
esterase	<i>Est</i> <sub>1</sub>	2 <sup>6</sup>	1 <sup>6</sup>		A
esterase	<i>Est</i> <sub>2</sub>	2 <sup>6</sup>	1 <sup>6</sup>		A
esterase	<i>Est</i> <sub>3</sub>	2 <sup>6</sup>	1 <sup>6</sup>		A
esterase	<i>Est</i> <sub>4</sub>	2 <sup>6</sup>	1 <sup>6</sup>		A
esterase	<i>Est.1</i>	2		3 <sup>7</sup>	E
esterase	<i>Est.2</i>	4		3 <sup>7</sup>	E
glucose 6-P deH	<i>G6pd</i>	2		3 <sup>7</sup>	E
$\alpha$ -glycero-P deH	<i>Gpd</i>	2	2	2	A
$\alpha$ -glycero-P deH	<i>Gpd.2</i>	2		3 <sup>7</sup>	E
leucine aminopeptidase	<i>lap</i> <sub>3</sub>	3	2	1 <sup>8</sup>	F
leucine aminopeptidase	<i>lap</i> <sub>3</sub>	4		3	A
malic deH	<i>Mdh.1</i>	2		3 <sup>7</sup>	E
malic enzyme	<i>Me</i>	4	2	1 <sup>9</sup>	F
octanol deH	<i>Odh</i>	3	3	2,3	D
xanthine oxidase	<i>Xo</i>	2	3	2,3	B

<sup>1</sup>Two bands in heterozygotes are interpreted as indicating that the active enzyme is a monomer, or that heterodimers are inactive. A pattern in which heterozygotes have three bands indicates that the active enzyme is a dimer; the band having the intermediate electrophoretic mobility being the heterodimer.

<sup>2</sup>Evidence abbreviated as follows: 1 = apparent agreement between observed and expected phenotype frequencies; 2 = population tested was in Hardy-Weinberg equilibrium; 3 = established by breeding experiments using two or more of the alleles.

<sup>3</sup>References abbreviated as follows: A = Geest *et al.* 1978; B = Rolseth and Gooding 1978; C = Gooding and Rolseth 1978; D = Gooding and Rolseth 1979; E = Gooding and Rolseth 1982; F = Geest and Kawooya 1975.

<sup>4</sup>Term *Ao* used independently by Geest *et al.* (1978) and by Rolseth and Gooding (1978), may not refer to the same locus; note difference in number of bands observed in heterozygotes.

<sup>5</sup>Although Geest *et al.* (1978) claim the population was in Hardy-Weinberg Equilibrium, the data they published do not support this claim.

<sup>6</sup>Flies had one band or no bands for these esterases and the existence of null-alleles was assumed by Geest *et al.* (1978). No analyses of the data were possible, nor were breeding experiments performed, to provide evidence for the genetic interpretation offered by Geest *et al.* (1978).

<sup>7</sup>Breeding data were not presented by Gooding and Rolseth (1982).

<sup>8</sup>Analysis of data published by Geest and Kawooya (1975) shows that criterion 3 (see footnote 1, above) has been met.

<sup>9</sup>Data published by Geest and Kawooya (1975) indicate the population was not in Hardy-Weinberg equilibrium.

rare allele was too low to permit one to determine whether the observed frequencies of phenotypes agreed with those predicted for a population in Hardy-Weinberg equilibrium. Similarly for another leucine aminopeptidase (*lap<sub>1</sub>*, Geest and Kawooya 1975) a single fly was found having two bands, while 479 flies had one band. The data do not permit testing of a genetic model. The *lap<sub>2</sub>* data were subsequently re-interpreted and it was proposed that the zone of staining represents enzymes controlled by two loci, one of which is monomorphic and the other has two alleles, one of which is extremely rare (Geest *et al.* 1978).

Electrophoretic variation has been found in at least 14 enzymes from *G. m. morsitans* and the data are summarized in Table 2. The exact number of enzymes, for which the genetics has been established, is in doubt because of difficulties in comparing work done by van der Geest and his co-workers, using starch gel, with work done in my laboratory, where polyacrylamide is used. We have both reported upon genetics of an aldehyde oxidase but, with our technique heterozygotes have three bands, while only two were found using starch gel. Thus these may not be the same aldehyde oxidase. Similarly it is not possible to determine whether the loci we have designated *Est.1* and *Est.2* (Gooding and Rolseth 1982) correspond to any of the esterase loci studied by Geest *et al.* (1978).

On starch gel electrophoresis 12 monomorphic loci and three polymorphic loci were found in *G. pallidipes* collected from natural populations at eight localities in Kenya (Etten 1982c). Monomorphic loci were found for the following enzymes (the designations for the loci are given in italics): two non-specific esterases (*est-2*, *est-3*) two leucine aminopeptidases (*lap-1*, *lap-2*); malic enzyme (*me*); alkaline phosphatase (*alph*); xanthine dehydrogenase (*x dh*); octanol dehydrogenase (*odh*); lactate dehydrogenase (*ldh*); malic acid dehydrogenase (*mdh*); isocitrate dehydrogenase (*idh*) and  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -gpd). Polymorphic loci occur for an esterase (*est-1*, 2 alleles), aldehyde oxidase (*ao*, 3 alleles), and a leucine aminopeptidase (*lap-3*, 4 alleles). Unfortunately the banding pattern in heterozygotes, and the existence of heterozygous males were not described by Etten (1982c).

As indicated above most of the information available on the genetics of electrophoretic mobility of enzymes comes from studies of *G. m. morsitans* but there have also been some comparative studies involving other taxa and most of these are summarized in Table 3. The banding patterns for most of these enzymes are the same as those found in the homologous enzymes in *G. m. morsitans* where genetic control of the enzyme mobility has been established by breeding experiments, suggesting that electrophoretic mobility of these enzymes is under genetic control in all the taxa studied.

Satellite DNA (=highly repetitive sequences) makes up about 8% of the total DNA in *G. m. morsitans* pupae and about 20% of the total in *G. austeni* (Dover 1980; Amos and Dover 1981). The figures for other species are: 16% for *G. pallidipes*, 9.6% for *G. f. fuscipes* and 14.8% for *G. tachinoides* (Dover 1980). Two bouyant density classes (1.678 g/cm<sup>3</sup> and 1.685 g/cm<sup>3</sup>) of satellite DNA occur in tsetse flies, the latter occurs in all taxa studied (i.e. five from *morsitans* group, four from *palpalis* group, and one from *fusca* group) while the former class of DNA occurs in all taxa except *G. austeni* (Dover 1980; Amos and Dover 1981). Experiments,

Table 3. Banding patterns found in various species by polyacrylamide gel electrophoresis.

Locus	No. bands in hetero- zygotes	Number of alleles in each taxon <sup>1</sup>								
		Gmc	Gmm	Gms	Gp	Ga	Gt	Gff	Gpg	Gpp
<i>Mdh.2</i>	U <sup>2</sup>	1	1 <sup>6</sup>	1	1	1	1	1	1	1
<i>To</i>	U <sup>2</sup>	1	1 <sup>6</sup>	1	1	1	1	1	1	1
<i>Apk</i>	2	1	2	1 <sup>7</sup>	1	1	1 <sup>7</sup>	1	1 <sup>7</sup>	1
<i>G6pd</i>	2	2	2	1	1	1	1	1	1	1
<i>Est.t</i>	N <sup>3</sup>	1	1 <sup>6</sup>	1	1	2	1	2	2	2
<i>Alkph</i>	2	2	2	1 <sup>7</sup>	3	2	3 <sup>8</sup>	1	3 <sup>8</sup>	1
<i>α-Gpd.2</i>	3	1	2 <sup>5</sup>	2 <sup>9</sup>	1	1	3 <sup>8</sup>	2	3 <sup>8</sup>	1
<i>Mdh.1</i>	3	1	2	3 <sup>8</sup>	1	1	3 <sup>8</sup>	1	3 <sup>8</sup>	2
<i>Est.1</i>	3 <sup>4</sup>	1	2 <sup>5</sup>	1	2	3	2	1	1	2
<i>Xo</i>	3	1	2	2	2	2	2	1	2	1
<i>Ao</i>	3	3	3	2	1	2	2	1	3	2
<i>Odh</i>	3	2	3	3 <sup>8</sup>	2	4	2 <sup>8</sup>	2	3 <sup>8</sup>	2

<sup>1</sup>Most of the data are from Gooding (1982b) and where indicated the data are supplemented with, or confirmed by, data from other publications. Names of the taxa are fully spelled out in Table 1.

<sup>2</sup>Unknown since in these monomorphic loci no heterozygotes have been found.

<sup>3</sup>Heterozygotes are non-existent since the locus *Est.1* is on the X chromosome. (See section on linkage groups.)

<sup>4</sup>Three bands occur but the fastest migrating homodimer stains only very faintly under normal conditions (Gooding 1984).

<sup>5</sup>A rare allele occurs at each of these loci in the Handeni line of *G. m. morsitans* (Gooding and Rolseth 1982).

<sup>6</sup>See also Gooding and Rolseth (1982).

<sup>7</sup>This situation was also found in flies from natural populations in Upper Volta (Gooding 1981a).

<sup>8</sup>Natural populations in Upper Volta had three alleles at each of these loci (Gooding 1981a).

<sup>9</sup>Two alleles occur in natural populations in Upper Volta (Gooding 1981a).

in which isotopically tagged satellite DNA was homologously hybridized to metaphase chromosomes, demonstrated that hybridization occurred mainly with B (=supernumerary) chromosomes but also with centromeres of autosome L<sub>1</sub> and X chromosome in *G. austeni*, all autosomes and both sex chromosomes in *G. m. morsitans*, and autosomes and X chromosomes (but possibly not the Y chromosome) in *G. pallidipes*. Tagged satellite DNA from *G. pallidipes* hybridized with autosomes and X chromosome of *G. m. morsitans* but not with either the Y chromosomes or B chromosomes. There was no appreciable hybridization between *G. austeni* satellite DNA and chromosomes of *G. m. morsitans*. The results indicate a closer

relationship between *G. m. morsitans* and *G. pallidipes* than between *G. m. morsitans* and *G. austeni*. These results also indicate that B chromosomes have arisen from A chromosomes within each species and that A and B chromosomes have evolved separately within a species, just as interspecific differences have arisen (Amos and Dover 1981).

### VECTERING ABILITY

The ability of tsetse flies to transmit trypanosomes is influenced by a number of factors (for reviews see Jordan 1974; Maudlin 1980), and there is little direct experimental evidence for genetic control of vectorial capacity. Arguing by analogy with the mosquito/*Plasmodium* and mosquito/filaria models, Jordan (1974) suggested that individual variation in susceptibility to trypanosomes may exist and that the most rewarding studies may involve transmission of *Trypanosoma congolense* group and *Trypanosoma brucei* group.

In each of several natural populations of four tsetse species, there was a higher prevalence of *Trypanosoma congolense* among males than among females. The reverse was found in one population of *G. pallidipes* (Clarke 1969). In three tsetse species, given the opportunity to become infected with *T. rhodesiense* under laboratory conditions, the prevalence of mature infections was higher in males than in females (Harley 1971). Although differences in susceptibility of males and females have been previously noted, no explanatory model has been proposed. The simplest explanation is that the difference in infection is attributable to many biochemical and physiological differences between male and female flies, and is not due to any one gene or small number of genes. Unfortunately such an explanation is difficult to test and unlikely to stimulate work on the subject.

The simplest genetic model to explain the sex difference in vectoring capacity is that it is due to an X chromosome locus. However this explanation is not quantitatively consistent with the data. If the allele conferring resistance were a recessive, all the available data sets (8 from Clarke 1969; 3 from Harley 1971) have a great excess of infected females. If susceptibility were due to a dominant allele, the same data sets, with one exception, are deficient in infected females. (The exception was *G. pallidipes* studied by Clark (1969), in which there was an excess of infected females.) The same discrepancies occur if one postulates involvement of two loci on the X chromosome.

A maternally influenced inheritance pattern for vectoring capacity, with apparently little or no dependence upon parental genotype, has been demonstrated in a laboratory colony of *G. m. morsitans* fed upon procyclic forms of *T. congolense* (Maudlin 1982). Males from the parental colony were slightly more susceptible to trypanosomes than were females, but the difference was not statistically significant. The nature of the maternal influence was not determined. In Maudlin's experiments 26.5% of the F<sub>1</sub> flies developed mature infections compared to 17.5% in the parental generation. The proportion of infective and non-infective females producing offspring, and number of offspring produced by each type of female do not explain the increase in mature infections in the F<sub>1</sub>. However this increase is consistent with the experimental design in which some F<sub>1</sub> flies were given more opportunities to become infected than were the parental generation. The effect of this experimental design upon the inheritance pattern is not discernable from the data.

Wild type *G. m. morsitans* males do not develop mature infections of *Trypanosoma brucei* (M'Pondi *et al. in prep*) or of *Trypanosoma congolense* (Distelmans *et al. in prep.*) as readily as do salmon *G. m. morsitans*. Although these results demonstrate a genetic influence



upon vectoring ability, it is not known whether this is a direct, specific effect on the trypanosomes, or a more general effect of the pleiotropic allele *salmon*. (See section on visible traits.)

## BEHAVIOURAL GENETICS

Tsetse flies present many opportunities for studying the genetics of behavioural phenomena (such as phototropism, circadian rhythms, habitat selection, host seeking, feeding and mating) which may have profound implications for control of these insects. However there have been few such studies.

Incursion of *G. tachinoides* into what are generally regarded as "atypical" habitats in Nigeria has been interpreted as indicating that this species may be more versatile, with respect to habitat selection, than had been previously suspected, and invasion of "atypical" habitats may have been due to (or may have resulted in) small genetic changes in the populations concerned (Baldry 1969). Unfortunately firm data on these points are lacking. (See section on interpopulation comparisons for information on genetics of natural populations of *G. tachinoides*.)

A comparison of various biological and metabolic parameters in *G. pallidipes* from Nkruman and Mwalewa, Kenya indicated that females in these populations feed at different frequencies (Etten 1982a). This difference was confirmed using females from the second generation of laboratory colonies (Etten 1982a) indicating that feeding frequencies are under genetic control. Similarly, the spontaneous activity of male *G. pallidipes* colonized from these two localities was different at both 24°C and at 30°C. In the field, activity of males during the early afternoon at Mwalewa was negatively correlated with temperature while at Nkruman there was no correlation between temperature and activity of males during the early afternoon. The results indicate that activity patterns and behavioural responses to temperature are under genetic control in *G. pallidipes* (Etten 1982b).

Duration of copulation is different in *G. pallidipes* from Kibwezi and Lambwe, Kenya (Jaenson 1978) and most of the difference is due to differences in the duration of the pre-transmission stage of copulation (Jaenson 1979a). Copulation duration in parental lines, in  $F_1$ , in  $F_2$ , and in backcrosses, indicates that this aspect of behaviour is controlled by genes on autosomes and on the X chromosome (with no evidence for involvement of the Y chromosome) and is mediated through the male (Jaenson 1978). Females also influence duration of copulation (Jaenson 1979b), but no genetic studies have established the number or location of the genes involved. In presenting data on polygenic control of copulation duration, Jaenson (1978) noted that the results were anomalous in that variance among  $F_2$  males was equal to that among  $F_1$  males, rather than the former being larger than the latter. Jaenson suggested that this "may be due to low heritability of the trait, interaction between genotype and environment and lack of homogeneity in the parental strains." Although this may be true, similar values for variances in  $F_1$  and  $F_2$  copulation time could also have been due to the rather small sample sizes (6 to 50 for  $F_1$ , 25 to 57 for  $F_2$ ) since, even if there were no recombination in the  $F_1$ , 18 different combinations of chromosomes are possible in  $F_2$  males, with the commonest type accounting for 12.5% of the sample.

Until recently the lack of suitable genetic markers prevented study of assortative mating within any *Glossina* taxon. (Assortative mating involving two taxa is reviewed in section on interspecific mating.) Even now only *G. m. morsitans* has genetic markers for such studies; the

two most convenient marker genes being *ocra* (body colour) and *salmon* (eye colour). The only published experiment indicated that assortative mating occurred in laboratory populations of salmon and wild type *G. m. morsitans* (Gooding 1982a). However, in this experiment the composition of the mating pairs was not determined by direct observation but rather by counting the number of each phenotype among  $F_1$  females. Another interpretation of the results is that, following multiple mating, there was preferential use of contypic sperm or differential mortality of larvae *in utero* which was influenced by the compatibility of maternal and progeny genotypes. Assortative mating is thus another aspect of behavioural genetics which remains to be investigated in tsetse.

## LINKAGE GROUPS

Although linkage groups are usually established through reciprocal crosses and/or the three-point-cross, electrophoretic techniques permit, under certain circumstances, assignment of a locus to either the X chromosome or the autosomes, without employing breeding experiments. This is possible since the structural genes on each chromosome, which are ultimately responsible for production of peptide chains, usually have co-dominant alleles. Thus, if a gene has electrophoretically detectable alleles, heterozygous males could occur only if the locus were on an autosome, but heterozygous females could occur if the locus were on either an autosome or the X chromosome. The criterion of heterozygotes in females, but not in males, was used to assign *Apk* (arginine phosphokinase, Gooding and Rolseth 1979) and *G6pd* (glucose 6-phosphate dehydrogenase, Gooding and Rolseth 1982) to the X chromosome of *G. m. morsitans*. Breeding experiments have confirmed the location of these loci. The existence of heterozygous males indicates that *lap-3* (the locus for leucine aminopeptidase-3) is on an autosome of *G. m. morsitans* (Geest *et al.* 1978).

On the basis of occurrence of heterozygotes in females but not in males, three loci have been assigned an X chromosome linkage and seven loci an autosomal linkage in several taxa (summarized in Table 4). For each locus, which has been assigned to either the X or the autosomes, the assignment has been the same in all taxa.

Breeding experiments established that *ocra* (body colour, Bolland *et al.* 1974; Gooding 1979) and *salmon* (eye colour, Gooding 1979) are located on the differential part of the X chromosome. Similarly, breeding experiments established that loci involved in determining the duration of copulation in *G. pallidipes* are spread among the autosomes and the X chromosome, but the number of loci and their exact location is unknown (Jaenson 1978; see section on behavioural genetics).

For *G. m. morsitans* four loci have been mapped in linkage group I (= X chromosome), seven have been mapped in linkage group II (an autosome), and one locus has been found in linkage group III (Gooding 1981b, 1983a, 1984). The linkage maps may be summarized as follows:

I(=X): *G6pd* <37.1 m.u.> *oc* <36.7 m.u.> *sal* <38.6 m.u.> *Apk*

II:  $\alpha$ -Gpd <45.0 m.u.> (*Xo/Alkph*) <45.7 m.u.> (*Ao/Odh*) <8 m.u.> [*Est.1/Est.2*]

III: *Mdh*

The region of the X chromosome which has been mapped does not involve the large paracentric inversion found in the "Handeni" line. In linkage group II the loci which are grouped together in parentheses ( ) are so close together that they have not yet been separated by genetical

Table 4. Assignment of loci to X chromosome or to autosomes based upon banding patterns.

Locus	Loci on X chromosome (X) or autosomes (A) in each taxon <sup>1</sup>								
	Gmc	Gmm	Gms	Gp	Ga	Gt	Gff	Gpg	Gpp
<i>Mdh.2</i>									
<i>To</i>									
<i>Apk</i>		X <sup>2</sup>							
<i>G6pd</i>	X	X <sup>3</sup>							
<i>Est.1</i>					X		X	X	X
<i>Alkph</i>	A	A <sup>4</sup>		A	A	A <sup>6</sup>		A <sup>6</sup>	
$\alpha$ -Gpd.2			A <sup>6</sup>			A <sup>6</sup>	A	A <sup>6</sup>	
<i>Mdh.1</i>		A <sup>3</sup>	A <sup>6</sup>			A <sup>6</sup>		A <sup>6</sup>	A
<i>Est.1</i>		A <sup>3</sup>		A	A	A			A
<i>Xo</i>		A <sup>5</sup>	A	A	A	A		A	
<i>Ao</i>	A	A <sup>5</sup>	A		A	A		A	A
<i>Odh</i>	A	A <sup>2</sup>	A <sup>6</sup>	A	A	A <sup>6</sup>	A	A <sup>6</sup>	A

<sup>1</sup>Most of the data are from Gooding (1982b) and where indicated the data are supplemented with, or confirmed by, data from other publications. A blank in the table means that the enzyme is monomorphic in that taxon and thus can not be assigned a linkage.

<sup>2</sup>Gooding and Rolseth (1979).

<sup>3</sup>Gooding and Rolseth (1982).

<sup>4</sup>Gooding and Rolseth (1978).

<sup>5</sup>Rolseth and Gooding (1978).

<sup>6</sup>Gooding (1981a).

recombination. The esterase loci [*Est.1/Est.2*] were located 5 to 10 m.u. to the right of *Ao* in two different experiments but are so close to each other, and the variances of the distances from *Ao* are so large, that the order of these loci remains in doubt.

During mapping experiments, no evidence was found for genetical recombination in males (Gooding 1981b, 1983a, 1984). However, since "chiasma-like configurations" occur at a low frequency during meiosis in *G. m. morsitans* (Craig-Cameron *et al.* 1973b) and chiasma occur in about 1% of male *G. f. fuscipes* (Pell and Southern 1976), genetical recombination may occur at very low frequencies in males of these species.

## POPULATION GENETICS

Population genetics may be considered as having two broad objectives: description of the genetics of a population or species; and an explanation of mechanisms responsible for maintenance of genetic variability within a population or species. The first objective may be subdivided into three more limited objectives: description of genotypes within a population; quantitative estimates of genetic variation within a population; and interpopulation comparisons of genetically determined traits. For practical purposes, each of these limited

objectives generally includes the previous objective and the literature reviewed will be treated accordingly. The second broad objective may be expanded to include explanations of evolutionary events and prediction of future events.

In reviewing the literature I have included some papers in which field observations suggest areas of interest to the study of population genetics, even though the observations themselves were not intended as contributions to population genetics.

### **Non-quantitative descriptions of single populations or species**

Polytene chromosome analysis has demonstrated inversions in the  $L_1L$  arm in some individuals in a laboratory colony of *G. pallidipes* (Southern and Pell 1981). Two forms of the Y chromosome have been demonstrated by Giemsa C-banding in *G. m. morsitans* and *G. m. submorsitans* (Southern and Pell 1981).

Three colour or pattern variations in the abdominal markings of *G. p. palpalis* have been associated with the habitat and/or geographic location in which the flies were found in Nigeria (Nash 1937). The general trend observed was for abdominal markings to become lighter as the vegetation becomes thinner. However it has not been established whether this is the result of natural selection or a direct environmental influence upon a polygenic trait or a trait with low heritability.

On the basis of variations in types of habitats occupied by *G. tachinoides* in Nigeria, Baldry (1969) suggested that this species is extremely versatile and that in certain localities it invaded "man-made environments" and became adapted to these. Baldry's proposal that there are many sub-populations of *G. tachinoides*, which ought to be amenable to analysis by the methods of population genetics, gains some support from Bursell's study of *G. morsitans*. In the latter species there are significant size differences in flies collected at sites that are only a few miles apart, suggesting that there is little movement by these flies (Bursell 1966). Body size in *G. m. morsitans* is influenced by both environmental and genetic factors (see section on visible traits) and there is significant selection against small males in natural populations in Zimbabwe (Phelps and Clarke 1974). The effects of this selection upon genetics of flies in natural populations might be worth investigating as it may relate to the problem of maintenance of polymorphisms in nature.

### **Estimates of genetic variation within a single population**

The first attempt to describe the amount of genetic variation within a species of tsetse was made by Geest *et al.* (1978) using starch gel electrophoretic techniques with *G. m. morsitans*. Twenty-three gene-enzyme systems were examined using flies from a colony whose ancestors came from Binga and Kariba districts in Zimbabwe. There was variation in mobility of 12 of the enzymes produced by the 23 to 28 loci examined, i.e. 43 to 52% of the loci were "polymorphic". (The exact number of loci is uncertain because of difficulties in interpreting the number of loci involved in producing double-banded, but non-varying, patterns for some enzymes.) Unfortunately, in this study most enzymes were reported only as varying or non-varying and allele frequencies were given for only three loci (*Ao*,  $\alpha$ -Gpd, and *lap*<sub>3</sub>). However it was concluded that mean heterozygosity was low "since in nearly all polymorphic loci, the most common allele occurs at a very high frequency" (Geest *et al.* 1978).

### Interpopulation comparisons

It is assumed, for the purposes of this discussion, that each self-sustaining laboratory colony is a separate population. In studies of field collected flies (or their  $F_1$  progeny) it is assumed that flies from each collection site are from a separate population. The latter is probably an oversimplification which may not be justified, despite the generally held view that tsetse flies do not move very far. (See for example Bursell 1966.)

Three laboratory populations (whose ancestors came from Handeni Tanzania, Kariba Zimbabwe, and Kariba-Binga Zimbabwe and involving the *ocra* mutation) were found to have a normal amount of variation among 14 loci examined by polyacrylamide gel electrophoresis (Gooding and Rolseth 1982). (This conclusion, documented below, is in contrast to the conclusion of Geest *et al.* (1978), that heterozygosity is low in colonies of *G. m. morsitans*.) The colonies did not differ significantly with regard to the number of polymorphic loci: 5-7 of 14 had a common allele with a frequency less than 99%; 4-6 of 14 had a common allele with a frequency less than 95%. Similarly the number of effective alleles per locus ( $1.43 \pm 0.62$  to  $1.79 \pm 0.94$ ) did not differ significantly among the colonies. However, the mean heterozygosity per locus ( $H$ ) was lower in flies from the Handeni colony ( $7.3 \pm 2.7\%$ ) than it was in flies from the other two colonies ( $16.7 \pm 5.7\%$  for Kariba,  $16.0 \pm 6.5\%$  for *ocra* colony). Female fecundity and longevity, and pupal weight are higher in the Kariba colony than in the Handeni colony (Jordan *et al.* 1977) while the performance of the *ocra* colony is reportedly as good as that of the Kariba line (Vloedt 1980). On the basis of allele frequency data (i.e. calculation of mean genetic identity, Nei 1972) it appears that the Kariba and *ocra* colonies are more closely related than either is to the Handeni colony (Gooding and Rolseth 1982). Thus the Handeni colony and the Kariba colony differ in mean heterozygosity and in frequency of various alleles. Cytogenetic differences between these strains had previously been demonstrated in regard to structure of the Y chromosome, presence of B chromosomes, Giemsa C-banding and an inversion on the X chromosome (Jordan *et al.* 1977). These genetic differences are consistent with the proposal by Jordan *et al.* (1977) that the reproductive differences between the colonies may be related to the genetically diverse nature of the two colonies but the genetic basis for differences in laboratory performance of the colonies has not been established.

Variations in Giemsa C-banding between three laboratory colonies (designated simply as colonies A, B, and C) of *G. m. morsitans* have been demonstrated (Southern and Pell 1981). The banding patterns in these colonies differ from those illustrated for the Kariba and Handeni lines (Jordan *et al.* 1977), thus there appear to be at least five (laboratory) populations of *G. m. morsitans* with regard to Giemsa C-banding patterns. The same technique has demonstrated two types of Y chromosomes in *G. m. morsitans* and *G. m. submorsitans* (Southern and Pell 1981) but the frequencies of each type within various laboratory populations has not been reported. Other cytogenetic differences between populations include variations in chromosome numbers for *G. pallidipes* from Lugala, Uganda ( $2n=6$ ) and from Kariba, Zimbabwe ( $2n=8$ ) (Maudlin 1970). The difference is probably due to the presence of B chromosomes in the Kariba population.

Sex chromosome aneuploidy was found in *G. p. palpalis* at five sites along the Niger and Kaduna rivers (Maudlin 1979; see section on sex determination.). No significant differences were found among flies from different sites (overall 21 of 249, or 8.4%, of females collected were shown to be XXY). However, at another site on the Zogruma Reserve, 200 km west of the study area mentioned above, only 2.4% of the female *G. p. palpalis* were XXY (Maudlin 1980). The frequency of sex chromosome aneuploidy in the populations studied is high

compared to the (expected) rate of spontaneous primary non-disjunction of X chromosomes in females, and this led Maudlin (1979) to conclude that aneuploidy is "maintained in the population as a polymorphism" by some as yet unknown mechanism.

Five enzyme systems have been studied by polyacrylamide gel electrophoresis in two natural populations of *G. m. submorsitans*, seven natural populations and two laboratory colonies of *G. p. gambiensis*, and four natural populations and one laboratory colony of *G. tachinoides* (Gooding 1981a). All the natural populations were from within 150 km of Bobo-Dioulasso, Upper Volta. All three species showed the same pattern for all five loci studied: at each locus there was a common allele, usually with a frequency greater than 93%, and each population had no more than two other alleles, and the frequency of the second commonest allele was always less than 6.5%. For each species, two of the five loci were polymorphic (i.e. frequency of commonest allele was less than 99%) while either zero or one (for *G. m. submorsitans*) of the five loci had a common allele with a frequency of less than 95%. For natural populations H values were low ( $3.49 \pm 2\%$  for *G. m. submorsitans*,  $2.45 \pm 1.26\%$  for *G. p. gambiensis*, and  $2.33 \pm 0.76\%$  for *G. tachinoides*). The low values for H are not because the loci chosen have intrinsically little variation in tsetse flies since in laboratory colonies of *G. m. morsitans* the H values for these loci (*Apk Odh Mdh*  $\alpha$ -Gpd and *Alkph*) vary from 9.4 to 20.4% (Gooding and Rolseth 1982). The reason for low heterozygosity among natural populations is unknown, but speculation has included both neutralist and selectionist interpretations of this polymorphism (Gooding 1981a).

Three of 15 enzyme loci were polymorphic in eight natural populations of *G. pallidipes* in Kenya (Etten 1982c). Mean heterozygosity per locus within these populations (calculated from data published by Etten) was rather low (2.4% to 5.7%) when compared to the value ( $12.2 \pm 5.4\%$ ) obtained in a laboratory colony originating from Uganda (Gooding 1982b), but was comparable to values found in natural populations of tsetse in Upper Volta (Gooding 1981a). The discrepancy between the heterozygosity in the laboratory and the natural populations of *G. pallidipes* probably is due to the lower resolving power of starch gel electrophoresis (used by Etten 1982c) when compared with polyacrylamide gel electrophoresis (used by Gooding 1982b). With one exception, the genotype frequencies in each population of *G. pallidipes* in Kenya differed from that of the neighbouring populations indicating restricted gene flow (Etten 1982c). Analysis (in my laboratory) of the allele frequency data, published by Etten (1982c), by a cluster analysis of the Nei's mean genetic identity values, showed that the grouping of populations, with two exceptions, did not correspond to the proximity of the populations to each other. This supports Etten's (1982c) conclusions but may be an indication of the hazards of making a comparison based upon few loci.

Comparisons limited to one or two traits or loci have limited value in comparing populations. However, for the sake of completeness a number of such studies will be mentioned here. *G. pallidipes* from the Lambwe Valley and from Kibwezi Forest Kenya, and flies in colonies established from these locations, differ in the duration of copulation (Jaenson 1978, 1979a). Similarly female *G. pallidipes* from Nkruman and Mwalewa Kenya feed at different frequencies (Etten 1982a; see section on behavioural genetics). Despite separation in the laboratory for about 25 generations (in each colony) *G. m. morsitans* maintained in the Department of Entomology, University of Alberta, were not significantly different from the (parental) colony at the Tsetse Research Laboratory, University of Bristol, when the frequency of genotypes were determined at the loci *Xo*, *Ao*, (Rolseth and Gooding 1978) and *Alkph* (Gooding and Rolseth 1978; see sections on biochemical and molecular genetics and on linkage

groups.). Similarly three laboratory colonies and a field colony examined at the *Lap*<sub>3</sub> locus were found to be similar (Geest *et al.* 1978). Although limited in scope, this study is interesting since two laboratory colonies and a field population from Zimbabwe were nearly identical, while the Handeni colony showed less genetic variation and had one less rare allele. (See similar comparison by Gooding and Rolseth (1982), cited above.)

### Intertaxon comparisons

Allele frequencies at 12 enzyme loci have been determined in colonies of nine taxa using polyacrylamide gel electrophoresis (Gooding 1982b). In each taxon in the *moristans* group four to eight of the loci were polymorphic, except in *G. m. submorsitans* where only two polymorphic loci were found. Within the *palpalis* group four or five of the loci were polymorphic in each taxon. Mean heterozygosity per locus was much lower in the *palpalis* group taxa (5.0 to 7.0%) than it was in most of the *morsitans* group taxa (11.7 to 21.0%). The exceptional subspecies in the later group was *G. m. submorsitans* which had a mean heterozygosity per locus of 2.4%. A phenogram based upon the allele frequencies in the colonies was, with two major exceptions, in agreement with the generally accepted arrangement of the taxa. The first exception was that *G. austeni* was clustered with members of the *palpalis* group rather than with the *morsitans* group. The second exception was that *G. m. submorsitans* (originating from Upper Volta) was less similar to *G. m. morsitans* and *G. m. centralis* than was *G. pallidipes*. (Other information derived from this comparative study is covered in sections on biochemical and molecular genetics and on linkage groups.)

### Population genetics and tsetse colonization

Much of the impetus for studying tsetse flies has come from the need to colonize these flies for use in control projects. This aspect of tsetse population genetics, and related matters, will be reviewed here. Because of the need for producing males which are competitive with field males, much of the work has been concerned with effects of prolonged colonization, inbreeding and/or adaptation to laboratory conditions. After two years of colonization (i.e. approximately 12 generations), *G. m. morsitans* released into the field had the same survival, dispersal, and rate of recapture as did field flies, and under laboratory conditions laboratory reared males were competitive with field males (Dame *et al.* 1975). A previously conducted laboratory evaluation of longevity, age specific fecundity, and puparial weights using this same species showed that females from a laboratory colony (a mixed population colonized for approximately 6 to 18 generations) were slightly superior to females emerging from field collected puparia (Jordan *et al.* 1970) but this difference may have been partly due to effects of shipping puparia. These experiments offer some assurances that colonization of *G. m. morsitans* for moderate lengths of time does not result in significant genetic drift or selection in medium to large colonies.

The possible consequences of intensive inbreeding have been studied using *G. austeni* (Jordan 1970) and *G. m. morsitans* (Jordan 1980). An inbred colony of the former species (consisting of 10 males and 10 females per generation) died out after 16 generations, but this was probably due to husbandry problems not related to inbreeding. The intensively inbred colony of *G. m. morsitans* lasted 40 generations without showing significant changes in female longevity, female fecundity, puparial weight, emergence rate or sex ratio (Jordan 1980). This colony began with a female mated to one male, and breeding stock for subsequent generations generally consisted of 10 females mated with three males. (Due to husbandry difficulties, not related to the inbreeding experiment, generation 14 consisted of only one female and her mate.)

By generation 40 the inbreeding coefficient was 0.9347, compared with 0.0303 for the parental colony. No morphological changes were found in the inbred colony (Jordan 1980) but by generation 26, flies were homozygous for malic enzyme and alkaline phosphatase, and 31 of 32 flies were homozygous for leucine aminopeptidase (Geest, in personal communication cited by Jordan 1980). By generation 40, xanthine oxidase, aldehyde oxidase (Rolseth and Gooding 1978) and alkaline phosphatase (which is probably different from that referred to above, Gooding and Rolseth 1978) were monomorphic. The frequencies of the alleles which became fixed rose from 0.36, 0.89 and 0.35 for *Ao*, *Xo*, and *Alkph* respectively. The results of the electrophoretic studies provide independent confirmation of the high value of the inbreeding coefficient calculated by Jordan (1980). The full significance of this inbreeding experiment is difficult to assess since it was not replicated and the female used to begin the experiment lived much longer and was much more productive than the average female.

Despite concerns about the effects of inbreeding, adaptation to the laboratory, genetic drift etc., little or no effort has been made to monitor genetic changes within tsetse colonies. Colony performance is usually gauged by puparial weights, female longevity and fecundity, emergence rates, and sex ratio at emergence. These are probably all polygenic characters, closely associated with fitness and probably with low heritability ( $h^2$ ). The use of electrophoretic techniques to monitor changes in tsetse colonies has been proposed, and techniques which permit examination of up to 12 loci from a single male have been developed (Gooding and Rolseth 1982). However, as far as I am aware, genetic monitoring of large colonies is not practiced and I doubt that such monitoring is likely in the absence of firm evidence that flies being produced within a colony differ significantly from field flies, or in the absence of a failure of laboratory reared flies to perform adequately under field conditions. *A propos*, a laboratory population of *G. p. gambiensis*, used to provide sterile males for an eradication project in Upper Volta, had less heterozygosity than, but was otherwise not significantly different from, a natural population adjacent to the site where a sterile male release program had been successfully carried out (Gooding 1981a). Nevertheless, further genetic studies on laboratory and field populations ought to be carried out to investigate what changes occur upon colonization of tsetse flies and the consequences of occasional introduction of field collected flies (or their offspring) into well-established colonies.

## GENETIC ASPECTS OF RADIATION AND CHEMOSTERILANTS

### General Aspects of Radiation Genetics

Exposing living organisms to X-irradiation or to  $\gamma$ -irradiation may cause somatic damage as well as a variety of genetic changes such as point mutations, chromosome rearrangements, and induced sterility through creation of dominant lethals. In this section I review the tsetse literature dealing with only the last three effects but do not cover the considerable amount of material which has been published on the use of the sterile male technique for control of tsetse flies.

In other organisms X- and  $\gamma$ -irradiation have been used to create mutants for genetic study, to create various chromosome aberrations as an aid to mapping loci, and to study the time of chromosome pairing and duplication. However, as far as I can determine from the literature, the first two approaches have not been attempted with tsetse flies.

The type of chromosome aberration induced by  $\gamma$ -irradiation depends upon the stage of meiosis at which irradiation is administered. For *G. m. morsitans* this has been established by irradiating females (with 700 rads using  $^{60}\text{Co}$ ) at various times during the second larviposition



cycle (Southern *et al.* 1975). (Under the conditions used, embryogenesis takes 96 to 120 hours, the first stadium lasts 26 h, the second stadium lasts 48 h, and larviposition takes place on the ninth or tenth day of the cycle.) Cytogenetic analysis of male progeny, nine to ten days after larviposition, established the following. The frequency with which translocations were created by radiation rose during the first 72 hours then declined to near zero by hour 120 of the larviposition cycle. The frequency of creating chromosome gaps and breaks (apparently induced in single-stranded chromosomes) rose in males irradiated during hours 48 to 120 then declined to near zero by hour 168 of the larviposition cycle. Chromatid aberrations begin to appear in males irradiated between hour 96 and 120; in flies irradiated between hours 144 and 168 these aberrations are the main, if not the only ones found. It was concluded by Southern *et al.* (1975) that by hour 144 chromosome duplication is advanced or even completed.

### Chromosome translocations

Curtis (1968a) outlined methods for creating chromosome translocations by treating post-teneral male tsetse flies with less than sterilizing doses of irradiation, and described methods for identifying lines carrying translocations by determining reduced fertility in progeny of outcrossed individuals. (He also discussed the practical uses of chromosome translocations as they might be applied to tsetse control. See also Curtis and Hill 1971, and Curtis and Robinson 1971.) Translocations were produced in *G. austeni* by exposing nine day old males to 5 to 7 krad  $^{60}\text{Co}$   $\gamma$ -irradiation and were identified, as indicated above, on the basis of inherited semi-sterility (Curtis 1969a). The semi-sterility occurred at a high frequency (ca. 34%) and in some lines was passed through males and females (and thus involved the autosomes) while in other families the inheritance pattern was holandric (indicating translocations involving the Y chromosome) (Curtis 1969a, 1969b, 1970b, 1971). Lines homozygous for translocation(s) (T/T) were believed to have been established (Curtis 1970b, 1971) but flies in at least some of these lines were less viable than wild type flies (Curtis 1971; Curtis *et al.* 1972). (The reduced viability was associated with reduced ability of T/T females to maintain normal pregnancies.) In two translocation lines the initial inheritance pattern indicated that the translocations involved autosomes, but after several generations there was a switch to a holandric inheritance pattern (Curtis 1971). Although several explanations were advanced, the nature of the switch-over was not established even though it was shown that after the switch-over the translocation involved the Y chromosome (Curtis *et al.* 1972). By examining some flies cytogenetically and their siblings by breeding experiments it was established (Curtis *et al.* 1972) that a translocation (in at least one line) caused partial sterility. Other lines with inherited partial sterility were also shown, by cytogenetic analysis, to have translocations (Curtis *et al.* 1972). In the cytogenetic studies cited above, and in work on *G. m. morsitans* reported by Curtis *et al.* (1973), the most common translocations involved exchange of segments from the long arms of  $L_1$  and  $L_2$ . Other translocations involved exchanges between supernumeraries and  $L_1$ , Y or other supernumeraries.

### Induction of Sterility by Irradiation

Most work on effects of radiation on tsetse flies has been directed towards induction of sterility in males by  $\gamma$ -irradiation and determination of somatic effects (notably effects on longevity and mating competitiveness) of this radiation. The work has been largely directed toward use of sterile males as control agents and the subject has been reviewed from this perspective several times (Dame 1970; Dame and Schmidt 1970; Jordan 1974, 1977, 1978;

Davidson 1978; Cuisance *et al.* 1980; Dame *et al.* 1980; Curtis and Langley 1982).

The preliminary work on radiation induced sterility used field collected puparia transported to laboratories in England (Potts 1958) or Zimbabwe (Dean *et al.* 1968; Dean and Wortham 1968; Dean and Clements 1969). Radiation induced sterility was first demonstrated in *G. morsitans* (probably *G. m. centralis* since the puparia were collected at Singida, Tanzania) by Potts (1958). These preliminary experiments were conducted under conditions which did not permit maintenance of self-sustaining colonies. The results indicated that about 65% of the males were sterilized by 5,760 rad when irradiated with  $\gamma$ -radiation from a  $^{60}\text{Co}$  source at some time during the last two thirds of the flies' life in the puparium. A decade later it was shown that greater than 95% sterility could be produced in male *G. m. morsitans* by  $\gamma$ -irradiation of puparia within a week or two of emergence with 8 to 15 krad (Dean *et al.* 1968; Dean and Wortham 1968). Irradiation of younger puparia resulted in sterilization at doses as low as 4 krad but under these conditions more profound somatic effects were induced. Female *G. m. morsitans* are sterilized by as little as one or two krad applied to either puparia or to one day old adults (Dean and Wortham 1968). Similar results were obtained with *G. pallidipes*: females were completely sterilized by exposure of puparia, one to two days before adult eclosion, to 4 krad and approximately 90% sterility was induced in males exposed to 5 to 18 krad within 10 days prior to eclosion. The greatest effects were observed when younger puparia were exposed to  $\gamma$ -radiation (Dean and Clements 1969).

Following establishment of tsetse colonies in Europe it was possible to conduct more precise experiments using flies of known age under conditions which were more nearly ideal for maintenance of the flies. (Selected data on levels of sterilization induced by various doses of irradiation are presented in Table 5.) These studies were largely directed towards perfection of sterile male release techniques but they also provided an understanding of mechanisms by which sterilization was induced.

The effectiveness of irradiation in sterilizing male insects may be explained by either of two models. The first proposes that irradiation kills sperm or prevents their production. During mating dead sperm and/or accessory gland secretions are passed to females which are thus rendered "sterile" by one of two mechanisms. As a result of a single act of mating (even with a sterilized male) the female may become refractory and never mate with other males available to her. Alternatively the female that mates with a sterilized male may have her spermathecae, or spermathecal ducts, filled with dead sperm and/or accessory gland secretions from the sterilized male and be unable to accept and store viable sperm from a normal male. The second model proposes that radiation produces dominant lethal mutations in sperm of treated males, and that such sperm are able to compete with normal sperm and fertilize eggs but that the resulting embryos fail to complete development.

The evidence available clearly establishes the second of the above mechanisms as the explanation for radiation induced sterility in male tsetse flies. Sperm are motile in radiation sterilized *G. m. morsitans* (Dean and Wortham 1968), *G. pallidipes* (Dean and Clements 1969) and *G. p. palpalis* (Hamann and Iwannek 1981). Females mated with radiation sterilized male *G. austeni* (Curtis 1968b, 1968c), *G. m. morsitans* and *G. tachinoides* (Itard 1970b, 1971a) will re-mate with normal males but produce few if any offspring.  $F_1$  flies descended from irradiated (partially sterilized) male *G. tachinoides* (Itard 1973a) or *G. m. morsitans* (Curtis *et al.* 1973) were either sterile or semi-sterile indicating that there had been genetic damage to their fathers. Further evidence that dominant lethals are being created by irradiation is distortion of sex ratio resulting in an excess of males among progeny of partially

Table 5. Sterilization of laboratory reared male tsetse flies by irradiation.<sup>1</sup>

Species	Stage irradiated (age, days)	krad	percent sterility	reference <sup>2</sup>
<i>austeni</i>	adult, 10	5	70	A
		7	90	A
		12	98	A
<i>m. morsitans</i>	adult, 1	20-25	100	B
	adult, 3	10.1	67	C D
		14.6	92	C D
	adult, 4	20	96	C D
		25	100	C D
	puparium, ca 30 <sup>3</sup>	7	72	E F
		10	92	E
		15	94	E F
		7 (in N)	60	E F
		10 (in N)	88	E F
		15 (in N)	94	E F
<i>palpalis</i>	adult, 4	11	94	G
		15 (in N)	94	G
<i>p. palpalis</i>	adult, 2	2 <sup>4</sup>	84	H
		5 <sup>4</sup>	94	H
		7.5-15 <sup>4</sup>	100	H
<i>tachinoides</i>	adult, 1-9	6	68	B C D
		10	95	B C D
		15	98	B C D

<sup>1</sup>Unless otherwise indicated, all data pertain to flies exposed to  $\gamma$ -irradiation in air. The data in this table are not a complete summary but only a representative sample.

<sup>2</sup>References: A=Curtis 1968c; B, C, D=Itard 1968, 1970b, 1971a; E=Langley *et al.* 1974; F=Curtis and 1972; G=Curtis and Langley 1982; H=Hamann and Iwannek 1981.

<sup>3</sup>Puparia from which almost all females had emerged were stored for five days at 11°C then irradiated in either air or nitrogen.

<sup>4</sup>Irradiated with  $\beta$ -irradiation.

sterilized male *G. austeni* (Curtis 1968c), *G. tachinoides* (Itard 1973a) and *G. m. morsitans* (Curtis *et al.* 1973). The latter study was the most complete and it was suggested by the authors that sperm carrying an X chromosome were more likely to have had a dominant lethal

induced in them than were the sperm carrying a Y chromosome. Calculations of the number of dominant lethals in male and female zygotes, and calculations of the relative lengths of the chromosomes most likely to be susceptible to induction of lethal mutations (i.e.  $L_1 + L_2 + X$  in female determining sperm and  $L_1 + L_2$  in male determining sperm) were in general agreement with the above interpretation (Curtis *et al.* 1973). Female *G. austeni* which mated twice (once with a normal male and once with a male sterilized by exposure to 12 krad of  $\gamma$ -radiation) used sperm from the first mating (regardless of whether this was with a normal or a sterilized male) for about 70% of the fertilizations. This clearly establishes that sperm from sterilized males were fully competitive with normal sperm (Curtis 1968b, 1968c). Female *G. p. palpalis* which mated with males sterilized by  $\gamma$ -radiation ovulated in a normal manner on the eighth or ninth day after emergence and histological examination showed that each egg was fertilized but that development usually ended at cleavage division (Matolin and Vloedt 1982). Only rarely did development proceed to gastrulation and development of a more or less fully formed embryo was even rarer.

### Induction of Sterility by Chemosterilants

The effects of aziridine chemosterilants on tsetse have been studied for about 20 years and a recent paper (Curtis and Langley 1982) summarized much of the information as it applies to control of tsetse by the sterile male release technique. Topical application (either directly or by having flies contact a previously treated surface) of apholate and metepa results in various levels of sterility in male and female *G. m. centralis* (Chadwick 1964). Similar experiments on *G. m. morsitans* have established the chemosterilizing ability of apholate (Dame *et al.* 1964), tepa (Dame *et al.* 1964, 1975; Dame and Ford 1966, 1967), metepa (Dame *et al.* 1964; Bursell 1977; House 1982) and bisazir (Coates and Langley 1982). Sterilization of male and female *G. pallidipes* by metepa has been demonstrated by House (1982).

Male *G. m. morsitans* are permanently sterilized by exposure to tepa (Dame and Ford 1966) and female *G. m. morsitans* mated to bisazir treated males do not regain fecundity with the passage of time (Coates and Langley 1982). After treatment with either of these chemosterilants sperm remain motile (Dame and Ford 1966; Coates and Langley 1982). From 14% to 45% of the fertilizations of twice mated *G. m. morsitans* females used sperm from the second mating, regardless of whether this or the first mating was with tepa sterilized males (Dame and Ford 1967). This indicates that the sperm of chemosterilized males are competitive with those of normal males. Some chemosterilant treated males fathered offspring which died within the puparia indicating that some of the lethal mutations induced by apholate and metepa in *G. m. centralis* (Chadwick 1964) and tepa in *G. m. morsitans* (Dame and Ford 1966) have an effect late in the development of the fly.

Several antibiotic sulfonamides interfere with reproduction of tsetse flies. The phenomenon has been studied most extensively in *G. austeni* and *G. m. morsitans* and the subject has been reviewed recently by Southern (1980). The sulfonamides cause degeneration of bacteroids in the midgut mycetome after flies have fed upon these compounds for about 19 days. About six to ten days later fragmentation of chromatin in nurse cells occurs but Rickettsia-like symbionts found in nurse cells and oocytes are not affected. The sulfonamides appear to adversely affect production of folic acid which is, among other things, a precursor of purines and thymine. This deficiency has an adverse effect upon DNA synthesis in polyploid nurse cells in which  $L_1$ ,  $L_2$ , and X chromosomes are replicating in the lampbrush state. The overall effect of this degeneration is that nurse and follicular cells are unable to synthesize and transfer to the oocyte

the ribosomes and transfer-RNA essential for embryogenesis and thus sterilization of the female tsetse results (Southern 1980).

## SOME GENETIC ASPECTS OF REPRODUCTION

### General Comments

Some aspects of mating behaviour and reproduction in tsetse flies appear to result from an attempt by each individual to increase the frequency of its genes in the next generation. Thus males will attempt to mate with as many females as possible and to induce monogamous behaviour in mated females. The major strategy of females is to protect and nourish their offspring until they have matured and are nearly ready to pupariate. Although females become monogamous, as a result of stimuli received from males, they do so gradually and thus retain, for some period of time, the ability to "hedge their bets" by mating with other males. One might consider that male and female tsetse flies are playing an evolutionary game with their partners: males divide their sperm production into aliquots of a certain size so as to maximize the number of potential mates, and females have spermathecae a little larger than necessary for storage of sperm from a single mating and are thus able to accept sperm from at least one additional male. Some consequences of this "evolutionary game" are considered below.

### Multiple mating by males

Multiple mating is to be expected in males of any organism but in tsetse flies, where meiosis occurs in pharate adults in the puparia, males are restricted in the number of females which they can successfully inseminate. *G. austeni* males, for example, can inseminate a maximum of 9 to 15 females (Curtis 1968b). The average volume of sperm transferred by *G. m. submorsitans* is 40% to 75% of the volume of the spermathecae and the amount transferred at the eighth mating is not significantly less than what is transferred at earlier matings (Pinhão 1980). Not all matings result in sperm transfer and with *G. m. submorsitans* from 7 to 23% of matings fail to result in sperm transfer and occasionally congenitally sterile males (i.e. those who never transfer sperm, though they mate repeatedly) are found (Pinhão 1980). Copulation without sperm transfer has also been observed with *G. pallidipes* (Jaenson 1979b). Whether these phenomena occur in the field as well as in the laboratory is not known. Individually marked male *G. pallidipes*, in the presence of females and other males in an observation chamber, vary considerably in the frequency with which they mate; some mate as often as four times in five hours while others do not mate at all (Rogers 1973a). There is no information available on the genetics of such variation.

### Multiple mating by females

Females which have mated are less receptive than are virgin females. The physiological basis for this is a combination of physical stimuli (stimulation of tactile receptors in female genitalia during mating and distension of the uterus by the developing larva) and chemical factors (from male accessory glands) transferred to the female at copulation (Gillott and Langley 1981). Nevertheless, females will mate more than once, especially if given an opportunity to do so within a day or two of the first mating. Multiple matings were first demonstrated under laboratory conditions in *G. p. palpalis* (Jordan 1958) and have subsequently been demonstrated in other species. About 40% of *G. pallidipes* females given an opportunity to mate every day for the first 13 days after eclosion, did so more than once, and such females were more fertile than were females that mated only once (Jaenson 1979b).

About 12% of wild *G. pallidipes* females which were observed *in copula* for 15 minutes at bait animals, and then forcibly separated from their mates, were found to be inseminated (presumably during a previous mating experience). This provides some evidence that multiple mating does occur in nature, in at least this species (Rogers 1973b).

#### Use of sperm by multiply mated females

Observing multiple mating by female tsetse flies is not proof that sperm are being transferred on each occasion, or that sperm from more than one mating can be effectively stored and used. Evidence for use of sperm from more than one mating requires marking sperm in some way. This has been accomplished by use of tepa sterilized male *G. m. morsitans* (Dame and Ford 1967), radiation sterilized male *G. austeni* (Curtis 1968b, 1968c, 1970a) and genetically marked (*ocra* vs. wild type) *G. m. morsitans* (Kawooya 1977; Vloedt 1980). These experiments established that sperm from both inseminations may be used but that at each pregnancy there is a greater probability of using sperm from the first mating than from the second. Almost all *G. austeni* females mated first to radiation sterilized males and then to normal males eventually became pregnant, indicating that virtually every female that mates twice has the capacity to use sperm from the second mating (Curtis 1968c). By scoring the offspring of individual females mated with two genetically different males it was established that some females used sperm from both matings (Kawooya 1977; Vloedt 1980; and unpublished work in my laboratory). Considering the frequency of multiple matings and the frequency of using sperm from the first mating, Kawooya (1977) estimated that, in populations where females have the opportunity for multiple mating, about 10 to 20% of the progeny will be from second matings.

Evidence for use of sperm from two matings in nature is limited to the single observation of a *G. m. centralis* female which was recaptured from *G. swynnertoni* habitat and which produced one male offspring having typical *morsitans*-type genitalia and another having genitalia typical of *morsitans/swynnertoni* hybrids (Vanderplank 1947). Since parthenogenesis does not occur in tsetse flies, this female must have mated with, and used sperm from, both *G. m. centralis* and *G. swynnertoni*. The extent to which use of sperm from two different matings occurs in nature might be resolved using electrophoretic techniques but the task would not be easy.

#### Interspecific mating

Results of hybridization experiments have indicated genetic similarities and taxonomic affinities among some of the taxa of tsetse flies, have demonstrated some of the mechanisms for preserving the genetic integrity of various taxa, and have begun to define the limits to incorporation of alien genes into the genomes of some species or subspecies.

Despite the fact that tsetse flies have sex recognition pheromones which appear to be species specific, intertaxon mating occurs rather extensively among tsetse flies under laboratory conditions (Vanderplank 1944, 1947, 1948; Curtis 1972; Huyton *et al.* 1980). In cages where flies had an opportunity to mate with their own or another species, *G. pallidipes* engaged only in conspecific matings while *G. m. centralis* and *G. swynnertoni* mated randomly resulting in a high insemination rate (92 to 96%) but in only 10 to 24% of females producing offspring (Vanderplank 1944, 1947). More surprising than this was the result of another experiment alluded to by Vanderplank (1947) in which an undisclosed number of male *G. swynnertoni* and *G. m. centralis* were individually identified and allowed to mate with females of either their

own or the other species. With one exception, each male engaging in a conspecific mating on the first occasion did so again on the second occasion, and each male engaging in an allospecific mating on the first occasion repeated this the second time. The exception was a *G. swynnertoni* male which changed from conspecific to allospecific mating. In the absence of a detailed description of the numbers of males and females used in the experiment it is difficult to speculate upon its significance. Nonetheless, this experiment raises the question of whether males, of these species, vary in their preference for mates, or, whether males mate randomly on the first occasion and learn from this an acceptable experience. The genetic aspects of either explanation may be well worth investigating.

There is sometimes a marked discrepancy between the tendency of males and females of a given species to engage in allospecific mating. *G. austeni* females are attractive to only *G. austeni* males and *G. tachinoides* females are attractive to only *G. tachinoides* and *G. austeni* males (Huyton *et al.* 1980). However, *G. austeni* males were attracted to, and attempted to mate with, at least some females from each of seven taxa with which the males were placed, and *G. tachinoides* males attempted to mate with *G. m. morsitans* and *G. p. palpalis* females as well as *G. tachinoides* females (Huyton *et al.* 1980).

The female behaviour mentioned above indicates one mechanism by which the genetic integrity of the species is preserved. Other prefertilization mechanisms known to occur in tsetse include the inability of *G. austeni* males to transfer sperm to *morsitans* group females because of the structure of the males' genitalia (Southern 1980). Similarly *palpalis* group males sometimes fail to transfer sperm during allospecific matings and those which transfer sperm usually puncture the abdomen of the females, with their claspers, causing death of the females (Vanderplank 1948).

Experiments on interspecific matings have also been carried out in the field. Jackson (1945) placed large numbers of *G. swynnertoni* puparia and *G. m. centralis* puparia in a *G. swynnertoni* habitat and later collected mating pairs within about 90 meters of the release site. The number of conspecific and allospecific pairs collected demonstrated that mating between these species was random. In a similar but less extensive experiment Vanderplank (1947) found a female *G. m. centralis* mating with a male *G. swynnertoni* after release of *G. m. centralis* into a *G. swynnertoni* habitat.

### Hybridization

Hybrids of closely related tsetse flies have been produced in the laboratory (Potts 1944; Vanderplank 1944, 1947, 1948; Curtis 1972; Southern and Pell 1973; Southern *et al.* 1973b; Curtis *et al.* 1980; Gooding 1982b) and evidence for hybridization in the field has been presented by Vanderplank (1947, 1949). The most complete tabulation of intertaxon matings, including those crosses which do and those which do not produce hybrid offspring, was presented by Vanderplank (1948). Earlier work on the subject (dating from 1907 to 1947) has been reviewed by Vanderplank (1948) and some of the later work has been reviewed by Southern (1980) and Curtis and Langley (1982). Practical implications of the subject have been reviewed by Jordan (1974) and Maudlin (1980).

In many hybridizing taxa there is a marked asymmetry in the suitability of females (Vanderplank 1944, 1947, 1948; Curtis 1972). For example the mating of *G. swynnertoni* females with *G. m. centralis* males produces far fewer offspring per female than does the reciprocal cross (Vanderplank 1944, 1947); mating *G. f. martinii* females with *G. f. fuscipes* males results in half as many females becoming pregnant as does the reciprocal cross

(Vanderplank 1948); and using *G. m. morsitans* males to inseminate either *G. m. centralis* or *G. morsitans submorsitans ugandensis* Vanderplank is far less likely to produce offspring than are either of the reciprocal crosses (Curtis 1972). These and other examples reported by Vanderplank (1948) suggest an interaction between the pregnant female and the embryo or larva which she is carrying. This suggestion is supported for the *G. f. fuscipes* / *G. f. martinii* model when one considers that, regardless of which species is the sperm donor, 93 to 100% of the eggs of the other species are fertilized *in vitro* and will develop to hatching, but *in vivo* hybridization produces far lower pregnancy rates (Vanderplank 1948). *In vitro* fertilization of eggs was accomplished for several species and in general the fertilization rate was higher than found for *in vivo* hybridization pregnancies (Vanderplank 1948). *In vitro* fertilization, like *in vivo* hybridization, occurred between taxa within a species group but never between taxa from different species groups (Vanderplank 1948).

### Maternal aspects of hybridization

Females mated to allospecific males have lower fertility than they would have had if they had mated with conspecific males (Vanderplank 1944, 1947, 1948; Curtis 1972; Curtis *et al.* 1980).  $F_1$  hybrid females, backcrossed to either parental taxon, show a further decline in fertility (Vanderplank 1948; Curtis 1972; Curtis *et al.* 1980), but fertility in hybrid females of subsequent generations (produced by repeated backcrosses to one parental taxon) rises as the genetic composition of the females approaches that of the ancestral taxon (Curtis 1972). Decreased female fertility is not due to cytoplasmic or chromosomal factors but rather it appears to be due to several loci resulting in some sort of genetic incompatibility between the mother and her offspring (Curtis 1972; Southern *et al.* 1973b). The nature of this incompatibility has not been elucidated but it should be noted that at least two sets of maternal gene products are transferred to the offspring. The first set consists of m-RNA, t-RNA, ribosomes *et cetera* produced by nurse cells and transmitted to oocytes. The second set consists of proteins, from the milk glands, which are fed to the larva *in utero*. There are ample opportunities for imbalances resulting from maternal and/or progeny genomes but none has yet been demonstrated.

### Paternal aspects of hybridization

$F_1$  hybrid males, regardless of their parentage, are unable to fertilize females (Vanderplank 1947, 1948; Curtis 1972). Hybrid males from the *palpalis* group are usually unable to successfully copulate because of spines on their claspers which kill their mates; if these spines are removed copulation can take place and the hybrid males are fertile (Vanderplank 1948). Vanderplank (1947, 1948) reported that  $F_1$  hybrid males from the *morsitans* group are able to transfer motile sperm to their mates but are, nonetheless, sterile. However, Curtis (1972) and Southern *et al.* (1973b), working with *G. morsitans* hybrids (*G. m. morsitans* X *G. m. centralis* or *G. m. submorsitans ugandensis*), reported that the  $F_1$  males were not able to inseminate females although they did have sperm with sub-normal mobility. The discrepancy, between the reports of Vanderplank (1947, 1948) and those of Curtis (1972) and Southern *et al.* (1973b), may be due to strain differences or to environmental differences during the experiments.

Meiosis in male hybrids of *G. morsitans* subspecies proceeds normally and there was pairing of  $L_1$  and of  $L_2$  chromosomes throughout their lengths. The pairing of the X and Y was characterized by the section of the Y, characteristic of the paternal taxon, associating with the



appropriate section of the X chromosome. F<sub>1</sub> male hybrid sterility clearly does not arise from errors at meiosis (Southern *et al.* 1973b, Southern and Pell 1973).

Hybrid males, produced by backcrossing F<sub>1</sub> females to a parental taxon, (i.e. B<sub>1</sub> males) may be classified as either sterile or fertile (Vanderplank 1948; Curtis 1972). The relative numbers of each of these types led Curtis (1972) to suggest that there is a single locus controlling male fertility (via sperm mobility) with each of the *G. morsitans* subspecies being characterized by a unique allele at that locus. The subject was explored further by using the X chromosome marker *ocra* (see section on visible traits) in *G. m. morsitans* which were crossed to *G. m. centralis*. B<sub>1</sub> males were scored for body colour and insemination ability. The results demonstrated involvement of the X chromosome in the ability of B<sub>1</sub> hybrid males to inseminate *G. m. morsitans* and *G. m. centralis* and suggested that for fertility there must be compatibility between the X chromosome and the Y and/or the autosomes (Curtis *et al.* 1980). The results were not as clear cut as might have been hoped and B<sub>1</sub> males capable of inseminating were found among both *ocra* and wild type males. It was suggested that this may have come about by genetic recombination in F<sub>1</sub> females resulting in separation of the marker locus, *ocra*, and the locus controlling sperm motility. However, a single, and rather limited, experiment found no evidence of genetic recombination in the region occupied by *ocra* and *salmon* on the X chromosome in hybrid F<sub>1</sub> (*G. m. morsitans* X *G. m. centralis*) females (Gooding 1982b). A more complete analysis of the genetic basis of male hybrid sterility must await creation of genetic strains which are appropriately marked at loci on each of the chromosomes.

### CONCLUDING REMARKS

Tsetse flies were among the first insects to be recognized as vectors of disease causing organisms (see review by Service 1978) and (according to Curtis and Langley, 1982) they were the first medically important insects against which genetic methods of control were directed. It is ironic therefore that genetic studies of tsetse flies have lagged so far behind those of other medically important insects. Reasons for this, and for its recent partial redress, were touched upon in the Introduction. During the past two decades considerable information has been acquired on the genetics of tsetse flies and the subject should no longer be considered as in its infancy. With the exception of the *fusca* group, genetic studies have passed beyond the purely descriptive stage and the search for markers, and they have now reached a point where they may be applied to answering fundamental questions about these flies.

Studies of tsetse genetics have been undertaken primarily because of the medical and veterinary importance of these insects. Such studies have already made contributions to the control of tsetse flies and it is to be hoped that further contributions will be forthcoming. There remains the question of whether genetic studies with tsetse flies will contribute anything unique to the field of genetics in general. If such contributions are to be made they are most likely to be in the areas of genetics of transmission of disease causing organisms, genetics of reproductive physiology, functions of the B chromosomes, and the relationship between tsetse flies and their symbionts. These seem to me to be potentially profitable areas of study for they are areas where tsetse flies are distinctly different from *Drosophila* species and from almost all other readily studied vector species.

## ACKNOWLEDGMENTS

I thank B.M. Rolseth for his assistance throughout this work, J.F. Landry for assistance in preparing the résumé, and B.S. Heming, Department of Entomology for constructive comments on the manuscript. This work was supported in part by a grant from the Natural Sciences and Engineering Research Council of Canada (Grant No. A-3900).

## REFERENCES

- Amos, A. and G. Dover. 1981. The distribution of repetitive DNAs between regular and supernumerary chromosomes in species of *Glossina* (tsetse): a two-step process in the origin of supernumeraries. *Chromosoma* (Berl.), 81:673-690.
- Baldry, D.A.T. 1969. Variations in the ecology of *Glossina* spp. with special reference to Nigerian populations of *Glossina tachinoides*. *Bulletin of the World Health Organization* 40:859-869.
- \_\_\_\_\_. 1970. A rapid staining technique for demonstrating the mitotic chromosomes of *Glossina* spp. pp349-354 in de Azevedo, J.F. (Editor). Tsetse fly breeding under laboratory conditions and its practical application. First International Symposium, 22nd and 23rd April 1969, 524pp. Lisbon, Junta de Investigações do Ultramar.
- Bolland, H.R., A. van Buren, L.P.S. van der Geest, and W. Helle. 1974. Marker mutation in the tsetse fly *glossina morsitans*. *Entomologia experimentalis et applicata* 17:522-524.
- Burchard, R.P. and D.A.T. Baldry. 1970. Polytene chromosomes of *Glossina palpalis* Robineau-Desvoidy. (Diptera: Muscidae). I. The preliminary demonstration. *Royal Entomological Society of London, Proceedings (A)* 45:182-183.
- Bursell, E. 1966. The nutritional state of tsetse flies from different vegetation types in Rhodesia. *Bulletin of Entomological Research* 57:171-180.
- \_\_\_\_\_. 1977. Chemosterilisation of tsetse flies using a pressurized metepa aerosol. *Rhodesian Scientific Association, Transactions* 58:43-47.
- Burt, E.D. 1944. A note on variation in living *Glossina brevipalpis* Newstead (Diptera), with particular reference to a red-coloured form found in nature. *Royal Entomological Society of London, Proceedings (A.)* 19:137.
- Buxton, P.A. 1955. *The Natural History of Tsetse Flies*. H.K. Lewis & Co. Ltd. London, xviii + 816 pp + 47 plates.
- Chadwick, P.R. 1964. Effect of two chemosterilants on *Glossina morsitans*. *Nature, London*. 204:299-300.
- Clarke, J.E. 1969. Trypanosome infection rates in the mouthparts of Zambian tsetse flies. *Annals of Tropical Medicine and Parasitology* 63:15-34.
- Coates, T.W. and P.A. Langley. 1982. Laboratory evaluation of contact sex pheromone and bisazir for autosterilization of *Glossina morsitans*. *Entomologia experimentalis et applicata* 31:276-284.
- Craig-Cameron, T.A., D.I. Southern, and P.E. Pell. 1973a. Chromosome ultrastructure at meiosis in *Glossina austeni* and *Glossina morsitans morsitans*. *Royal Society of Tropical Medicine and Hygiene (London), Transactions* 67:303-304.
- \_\_\_\_\_. 1973b. Chiasmata and the synaptonemal complex in male meiosis of *Glossina*. *Cytobios* 8:199-207.
- \_\_\_\_\_. 1974. Vesicle

- ultrastructure and RNA synthesis during male meiosis of *Glossina austeni* (Diptera, Glossinidae). *Cytobios* 9:13-21.
- Cuisance, D., H. Politzar, M. Clair, E. Sellin, Y. Taze, G. Bourdoiseau, et J. Fevrier. 1980. La lutte contre *Glossina palpalis gambiensis* Vanderplank par lâchers de mâles irradiés en Haute-Volta. in *Isotope and Radiation Research on Animal Diseases and Their Vectors*. International Atomic Energy Agency (Vienna) STI/PUB/525: 249-266.
- Curtis, C.F. 1968a. A possible genetic method for the control of insect pests, with special reference to tsetse flies (*Glossina* spp.). *Bulletin of Entomological Research* 57:509-523.
- \_\_\_\_\_. 1968b. Some observations on reproduction and the effects of radiation on *Glossina austeni*. Royal Society of Tropical Medicine and Hygiene (London), *Transactions* 62:124.
- \_\_\_\_\_. 1968c. Radiation sterilization and the effect of multiple mating of females of *Glossina austeni*. *Journal of Insect Physiology* 14:1365-1380.
- \_\_\_\_\_. 1969a. The production of partially sterile mutants in *Glossina austeni*. *Genetical Research* (Cambridge) 13:289-301.
- \_\_\_\_\_. 1969b. Attempt to produce chromosome translocations in tsetse flies. *Heredity* 24:175.
- \_\_\_\_\_. 1970a. The expression of induced sterility in *Glossina austeni*. Royal Society of Tropical Medicine and Hygiene (London), *Transactions* 64:186.
- \_\_\_\_\_. 1970b. An attempt to produce stocks homozygous for chromosome translocations in *Glossina austeni*. pp355-360 in de Azevedo, J.F. (Editor). *Tsetse fly breeding under laboratory conditions and its practical application*. First International Symposium, 22nd and 23rd April 1969, 524pp. Lisbon, Junta de Investigacoes do Ultramar.
- \_\_\_\_\_. 1971. Experiments on breeding translocation homozygotes in tsetse flies. in *Sterility Principle for Insect Control or Eradication*. International Atomic Energy Agency (Vienna) STI/PUB/265: 425-435.
- \_\_\_\_\_. 1972. Sterility from crosses between sub-species of the tsetse fly, *Glossina morsitans*. *Acta Tropica*. 29:250-268.
- Curtis, C.F. and W.G. Hill. 1971. Theoretical studies on the use of translocations for the control of tsetse flies and other disease vectors. *Theoretical Population Biology* 2:71-90.
- \_\_\_\_\_. and P.A. Langley. 1972. Use of Nitrogen and chilling in the production of radiation-induced sterility in the tsetse fly *Glossina morsitans*. *Entomologia experimentalis et applicata* 15:360-376.
- \_\_\_\_\_. 1982. Sterility induction in tsetse. in *Sterile Insect Technique and Radiation in Insect Control*. International Atomic Energy Agency (Vienna). STI/PUB/595: 169-183.
- \_\_\_\_\_, A.R. Mews, E.D. Offori, D.I. Southern, and P.E. Bell. 1973. Sex ratio distortion and semi-sterility in the progeny of irradiated *Glossina morsitans*. *Genetical Research* (Cambridge) 21:153-165.
- \_\_\_\_\_, and M.A. Trewern. 1980. X-chromosome involvement in male hybrid sterility from *Glossina morsitans* sub-species crosses. *Heredity* 45:405-410.
- \_\_\_\_\_, and A.S. Robinson. 1971. Computer simulation of the use of double translocations for pest control. *Genetics* 69:97-113
- \_\_\_\_\_, D.I. Southern, P.E. Pell, and T.A. Craig-Cameron. 1972. Chromosome translocations in *Glossina austeni*. *Genetical Research* (Cambridge) 20:101-113.

- Dame, D.A. 1970. Control by sterilization of *Glossina*. Chapt. 26 (pp533-542) in H.W. Mulligan (Editor) The African Trypanosomiasis, George Allen and Unwin Ltd., London, lxxxviii + 950pp.
- \_\_\_\_\_, D.R. Birkenmeyer, T.A.M. Nash, and A.M. Jordan. 1975. The dispersal and survival of laboratory-bred and native *Glossina morsitans morsitans* Westw. (Diptera, Glossinidae) in the field. Bulletin of Entomological Research 65:453-457.
- \_\_\_\_\_, G.J.W. Dean, and J. Ford. 1964. Investigations of the sterile male technique with *Glossina morsitans*. International Scientific Committee for Trypanosomiasis Research (Kampala, Uganda), Proceedings of Tenth Meeting: 93-96.
- \_\_\_\_\_, and H.R. Ford. 1966. Effect of the chemosterilant tepa on *Glossina morsitans* Westw. Bulletin of Entomological Research 56:649-658.
- \_\_\_\_\_. 1967. Multiple mating of *Glossina morsitans* Westw. and its potential effect on the sterile male technique. Bulletin of Entomological Research 58:213-219.
- \_\_\_\_\_, and C.H. Schmidt. 1970. The sterile-male technique against tsetse flies, *Glossina* spp. Bulletin of the Entomological Society of America 16:24-30.
- \_\_\_\_\_, D.L. Williamson, P.E. Cobb, D.B. Gates, P.V. Warner, A.G. Mtuya, and H. Baumgartner. 1980. Integration of sterile insects and pesticides for the control of the tsetse fly *Glossina morsitans morsitans*. in Isotope and Radiation Research on Animal Diseases and Their Vectors. International Atomic Energy Agency (Vienna) STI/PUB/525: 267-280.
- Davidson, G. 1978. Prospects of genetic control for medically important insects. pp111-119 in Willmott, S.(Editor). Medical Entomology Centenary, 23rd to 25th November 1977 London, U.K. Royal Society of Tropical Medicine and Hygiene (London), Symposium Proceedings.
- Davies, E.D.G. and D.I. Southern. 1976. Giemsa C-banding within the genus *Glossina* (Diptera, Glossinidae). Genetica 46:413-418.
- \_\_\_\_\_. 1977. Female meiosis in two species of tsetse fly (genus *Glossina*). Genetica 47:173-175
- Davis, J.C. and R.H. Gooding. 1983. Spectral sensitivity and flicker fusion frequencies of the compound eye of salmon and wild-type tsetse flies, *Glossina morsitans*. Physiological Entomology 8:15-23.
- Dean, G.J.W. and S.A. Clements. 1969. Effect of gamma-radiation on *Glossina pallidipes* Aust. Bulletin of Entomological Research 58:755-761.
- \_\_\_\_\_, D.A. Dame, and D.R. Birkenmeyer. 1968. Field cage evaluation of the competitiveness of male *Glossina morsitans orientalis* Vanderplank sterilised with tepa or gamma irradiation. Bulletin of Entomological Research 59:339-344.
- Dean, G.J. and S.M. Wortham. 1968. Effect of gamma-radiation on the tsetse fly *Glossina morsitans* Westw. Bulletin of Entomological Research 58:505-519
- Distelmans, W., A. Makumyavari M'Pondi, D. Le Ray, and R.H. Gooding. (in prep.) Influence of the salmon mutant of *Glossina morsitans morsitans* on the susceptibility to infection with *Trypanosoma congolense*.
- Dover, G. 1980. The evolution of DNA sequences common to closely-related insect genomes. pp 13-35 in R.L. Blackman, C.W. Hewitt, and M. Ashburner (Editors) Insect Cytogenetics. Blackwell Scientific Publishers, Oxford.
- Etten, J. van. 1982a. Comparative studies on fat reserves, feeding and metabolic strategies of flies from two allopatric populations of *Glossina pallidipes* Austen in Kenya. Acta Tropica

39:157-169.

- 
- \_\_\_\_\_. 1982b. Comparative studies on the diurnal activity pattern in two field and laboratory populations of *Glossina pallidipes*. *Entomologia experimentalis et applicata* 32:38-45.
- 
- \_\_\_\_\_. 1982c. Enzyme polymorphism in populations of the tsetse fly *Glossina pallidipes* in Kenya. *Entomologia experimentalis et applicata* 31:197-201.
- Geest, L.P.S. van der, A. Cornelissen, H.P. Tjon-a-joe, and W. Helle. 1978. A study on isoenzyme polymorphism in the tsetse fly *Glossina morsitans*. *Entomologia experimentalis et applicata*. 23:269-278.
- 
- \_\_\_\_\_. and J. Kawooya. 1975. Genetic variation in some enzyme systems in the tsetse fly *Glossina morsitans*. *Entomologia experimentalis et applicata*. 18:508-514.
- Gillott, C. and P.A. Langley. 1981. The control of receptivity and ovulation in the tsetse fly, *Glossina morsitans*. *Physiological Entomology* 6:269-281.
- Glasgow, J.P. 1963. The Distribution and Abundance of Tsetse. (see Chapt. 12 (pp 160-169), The variations of tsetses in nature.) Macmillan N.Y. xi + 241pp.
- 
- \_\_\_\_\_. 1970. The genus *Glossina*: Introduction. Chapt. 8 (pp225-242) in H.W. Mulligan (Editor) *The African Trypanosomiasis*. George Allen and Unwin Ltd., London, lxxxviii + 950 pp.
- Gooding, R.H. 1978. A possibility for genetic control of tsetse. *Entomological Society of Alberta, Proceedings* 26:22.
- 
- \_\_\_\_\_. 1979. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae) III. *salmon*, a sex-linked, maternally influenced, semi-lethal eye color mutant. *Canadian Entomologist* 111:557-560.
- 
- \_\_\_\_\_. 1981a. Genetic polymorphism in three species of tsetse flies (Diptera: Glossinidae) in Upper Volta. *Acta Tropica*. 38:149-161.
- 
- \_\_\_\_\_. 1981b. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). V. Definition and preliminary mapping of linkage groups I and II. *Canadian Journal of Genetics and Cytology* 23:399-403.
- 
- \_\_\_\_\_. 1982a. Laboratory evaluation of the lethal allele *salmon* for genetic control of the tsetse fly, *Glossina morsitans morsitans*. in *Sterile Insect Technique and Radiation in Insect Control*. International Atomic Energy Agency (Vienna). STI/PUB/595: 267-278.
- 
- \_\_\_\_\_. 1982b. Classification on nine species and subspecies of tsetse flies (Diptera: Glossinidae: *Glossina* Wiedemann) based on molecular genetics and breeding data. *Canadian Journal of Zoology* 60:2737-2744.
- 
- \_\_\_\_\_. 1983a. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). VII. Location of *G6pd* in linkage group I, and *Alkph* in linkage group II. *Canadian Journal of Genetics and Cytology* 25:30-32.
- 
- \_\_\_\_\_. 1983b. Preliminary observations on behaviour of salmon-eyed male *Glossina morsitans morsitans*. *Entomological Society of Alberta, Proceedings* 30:12.
- 
- \_\_\_\_\_. 1984. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). IX. Definition of linkage group III and further mapping of linkage groups I and II. *Canadian Journal of Genetics and Cytology* (in press).
- 
- \_\_\_\_\_. and J.E. Hollebhone. 1976. Heritability of adult weight in the tsetse fly *Glossina morsitans morsitans* Westw. (Diptera: Glossinidae). *Experientia*. 32:1507-1508.
-

- 
- \_\_\_\_\_. and B.M. Rolseth. 1978. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae) II. Electrophoretic banding patterns of midgut alkaline phosphatase. Canadian Entomologist 110:1241-1246.
- 
- \_\_\_\_\_. 1979. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae) IV. Electrophoretic banding patterns of octanol dehydrogenase and arginine phosphokinase. Canadian Entomologist 111:1307-1310.
- 
- \_\_\_\_\_. 1982. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). VI. Multilocus comparison of three laboratory populations. Canadian Journal of Genetics and Cytology 24:109-115.
- 
- \_\_\_\_\_. 1984. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae). VIII. Tryptophan oxygenase deficiency, the lesion causing salmon-colored eyes. Canadian Journal of Genetics and Cytology 26:62-66.
- Hamann, H.J. and K.H. Iwanek. 1981. Sterilisation of *Glossina palpalis palpalis* (Robineau-Desvoidy) (Diptera: Glossinidae) by beta irradiation. Bulletin of Entomological Research 71:513-517.
- Harley, J.M.B. 1971. Comparison of the susceptibility to infection with *Trypanosoma rhodesiense* of *Glossina pallidipes*, *G. morsitans*, *G. fuscipes*, and *G. brevipalpis*. Annals of Tropical Medicine and Parasitology 65:185-189.
- House, A.P.R. 1982. Chemosterilisation of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera: Glossinidae) in the field. Bulletin of Entomological Research 72:65-70.
- Hulley, P.E. 1968. Mitotic chromosomes of *Glossina pallidipes* Austen. Nature, London. 217:977-979.
- Huyton, P.M., P.A. Langley, D.A. Carlson, and M. Schwarz. 1980. Specificity of contact sex pheromones in tsetse flies, *Glossina* spp. Physiological Entomology 5:253-264.
- Itard, J. 1966. Chromosomes de Glossines (Diptera-Muscidae). Academie des Sciences (France), Comptes Rendus Hebdomadaires des Sciences. Serie D. Sciences Naturelles 263:1395-1397.
- 
- \_\_\_\_\_. 1968. Stérilisation des mâles de *Glossina tachinoides* West. par irradiation aux rayons gamma. Revue D'Elevage et de Médecine Vétérinaire des Pays Tropicaux 21:479-491.
- 
- \_\_\_\_\_. 1970a. Les caryotypes de six espèces de Glossines. pp 361-367 in de Azevedo, J.F. (Editor). Tsetse fly breeding under laboratory conditions and its practical application. First International Symposium, 22nd and 23rd April 1969, 524pp. Lisbon, Junta de Investigações do Ultramar.
- 
- \_\_\_\_\_. 1970b. Stérilisation des mâles de *Glossina morsitans morsitans* et de *G. tachinoides* West. par irradiation aux rayons gamma. pp 369-383 in de Azevedo, J.F. (Editor). Tsetse fly breeding under laboratory conditions and its practical application. First International Symposium, 22nd and 23rd April 1969, 524pp. Lisbon, Junta de Investigações do Ultramar.
- 
- \_\_\_\_\_. 1971a. Elevage, cytogénétique et spermatogénèse des insectes du genre *Glossina*. Stérilisation des mâles par irradiation gamma. Annales de Parasitologie Humaine et Comparée (Paris), 46, 3 bis: 35-66.
- 
- \_\_\_\_\_. 1971b. L'appareil reproducteur mâle des Glossines (Diptera, Muscidae). Les étapes de sa formation chez la pupa. La spermatogénèse. Revue D'Elevage et de Médecine Vétérinaire des Pays Tropicaux 23:57-81.

- \_\_\_\_\_. 1971c. Chromosomes de *Glossina fusca congolensis* Newstead et Evans, 1921 (Diptera-Muscidae). Academie des Sciences (France), Comptes Rendus Hebdomadaires des Sciences. Serie D. Sciences Naturelles 272:2561-2564.
- \_\_\_\_\_. 1973a. Sterilisation by gamma irradiation of adult male glossinae low dosage irradiation (4,000 to 6,000 'rads') of adult male *G. tachinoides*. International Scientific Committee for Trypanosomiasis Research (Lagos, Nigeria), Proceedings of Thirteenth Meeting: 321-325.
- \_\_\_\_\_. 1973b. Revue des connaissances actuelles sur la cytogenétique des Glossines (Diptera). Revue D'Elevage et de Médecine Vétérinaire des Pays Tropicaux 26:151-167.
- \_\_\_\_\_. 1974. Caryotype de *Glossina palpalis gambiensis* Vanderplank, 1949. Comparaison avec d'autres espèces du groupe *palpalis* et du groupe *morsitans*. Revue D'Elevage et de Médecine Vétérinaire des Pays Tropicaux 27:431-436.
- Jackson, C.H.N. 1945. Pairing of *Glossina morsitans* Westwood with *G. swynnertoni* Austen (Diptera). Royal Entomological Society of London, Proceedings (A) 20:106.
- Jaenson, T.G.T. 1978. Mating behaviour of *Glossina pallidipes* Austen (Diptera, Glossinidae): Genetic differences in copulation time between allopatric populations. Entomologia experimentalis et applicata. 24:100-108.
- \_\_\_\_\_. 1979a. Mating behaviour of males of *Glossina pallidipes* Austen (Diptera: Glossinidae). Bulletin of Entomological Research 69:573-588.
- Jaenson, T.G.T. 1979b. Mating behaviour of *Glossina pallidipes* (Diptera, Glossinidae): Duration of copulation, insemination and fecundity. Entomologia experimentalis et applicata. 26:1-12.
- Jordan, A.M. 1958. The mating behaviour of females of *Glossina palpalis* (R.-D.) in captivity. Bulletin of Entomological Research 49:35-43.
- \_\_\_\_\_. 1970. Inbreeding of *Glossina austeni*. pp 137-141 in de Azevedo, J.F. (Editor). Tsetse fly breeding under laboratory conditions and its practical application. First International Symposium, 22nd and 23rd April 1969, 524pp. Lisbon, Junta de Investigacoes do Ultramar.
- \_\_\_\_\_. 1974. Recent developments in the ecology and methods of control of tsetse flies (*Glossina* spp.) (Dipt., Glossinidae)-a review. Bulletin of Entomological Research 63:361-399.
- \_\_\_\_\_. 1977. Systematics. pp.13-22 in M. Laird (Editor) "Tsetse: the future for biological methods in integrated control." Ottawa, International Development Research Centre -077c 1977. 220pp.
- Jordan, A.M. 1978. Recent developments in techniques for tsetse control. p76-84 in Willmott, S.(Editor). Medical Entomology Centenary, 23rd to 25th November 1977 London, U.K. Royal Society of Tropical Medicine and Hygiene (London), Symposium Proceedings.
- \_\_\_\_\_. 1980. Forty generations of inbreeding of *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae). Bulletin of Entomological Research 70:557-562.
- \_\_\_\_\_, T.A.M. Nash, and M.A. Trewern 1970. The performance of crosses between wild and laboratory-bred *Glossina morsitans orientalis* Vanderplank. Bulletin of Entomological Research 60:333-337.
- \_\_\_\_\_, M.A. Trewern, D.I. Southern, P.E. Pell, and E.D.G. Davies. 1977. Differences in laboratory performance between strains of *Glossina morsitans morsitans* Westwood from Rhodesia and Tanzania and associated chromosome diversity. Bulletin of Entomological Research 67:35-48.

- Kawooya, J. 1977. Demonstration of multiple insemination in females of *Glossina morsitans* Westwood, using a phenotype genetic marker Ocr. *Zeitschrift fur Angewandte Entomologie* 84:321-327.
- Langley, P.A. 1977. Physiology of tsetse flies (*Glossina* spp.) (Diptera: Glossinidae): a review. *Bulletin of Entomological Research* 67:523-574.
- \_\_\_\_\_, C.F. Curtis, and J. Brady. 1974. The viability, fertility and behaviour of tsetse flies (*Glossina morsitans*) sterilized by irradiation under various conditions. *Entomologia experimentalis et applicata*. 17:97-111.
- Matolin, S. and A.M.V. van der Vloedt. 1982. Changes in the egg of the tsetse fly, *Glossina palpalis palpalis* (Diptera: Glossinidae), after fertilization by sperm of gamma-irradiated males. in *Sterile Insect Technique and Radiation in Insect Control*. International Atomic Energy Agency (Vienna). STI/PUB/595: 155-168.
- Maudlin, I. 1968. Chromosomes of the tsetse fly *Glossina fuscipes fuscipes* (Newstead). East African Trypanosomiasis Research Organization, Annual Report. 1968:64-66.
- \_\_\_\_\_. 1970. Preliminary studies on the karyotypes of five species of *Glossina*. *Parasitology*. 61:71-74.
- \_\_\_\_\_. 1979. Chromosome polymorphism and sex determination in a wild population of tsetse. *Nature, London* 277:300-301.
- \_\_\_\_\_. 1980. Population genetics of tsetse flies and its relevance to trypanosomiasis research. *Insect Science and its Application* 1:35-38.
- \_\_\_\_\_. 1982. Inheritance of susceptibility to *Trypanosoma congolense* infection in *Glossina morsitans*. *Annals of Tropical Medicine and Parasitology* 76:225-227.
- M'Pondi, A.M., W. Distelmans, Y. Claes, F. D'Haeselfer, D. Le Ray, and R.H. Gooding. (in prep.) *Trypanosoma brucei*: Capacité vectorielle du type sauvage et du mutant "salmon" de *Glossina morsitans morsitans* (Diptera: Glossinidae).
- Nash, T.A.M. 1937. Abdominal markings in the genus *Glossina* (Diptera), in relation to habitat. *Zoological Society of London, Proceedings (A)* 107:351-352.
- Newstead, J.R., A.M. Evans, and W.H. Potts. 1924. Guide to the study of tsetse flies. *Memoires Liverpool School of Tropical Medicine (new series 1)*, 332 pp.
- Nei, M. 1972. Genetic distance between populations. *American Naturalist* 106:283-292.
- Pell, P.E. and D.I. Southern. 1976. A cytogenetical study of *Glossina fuscipes fuscipes* including a comparison of the polytene chromosome maps with those of *Glossina austeni* (Diptera, Glossinidae). *Genetica* 46:511-528.
- \_\_\_\_\_, D.I. Southern, and T.A. Craig-Cameron. 1973. Comparative cytogenetics of the *Glossina morsitans* group. *Royal Society of Tropical Medicine and Hygiene (London), Transactions* 67:302-303.
- Phelps, R.J. and G.P.Y. Clarke. 1974. Seasonal elimination of some size classes in males of *Glossina morsitans morsitans* Westw. (Diptera, Glossinidae). *Bulletin of Entomological Research* 64:313-324.
- Pinhão, R.C. 1980. La multiplicité des accouplements chez les glossines et la methode des lâchers de mâles stériles. in *Isotope and Radiation Research on Animal Diseases and their Vectors*. International Atomic Energy Agency (Vienna) STI/PUB/525: 397-407.
- Potts, W.H. 1944. Tsetse Hybrids. *Nature, London* 154:606-607.
- \_\_\_\_\_. 1958. Sterilization of tsetse-flies (*Glossina*) by gamma irradiation. *Annals of Tropical Medicine and Parasitology* 52:484-499.
- \_\_\_\_\_. 1973. Glossinidae (Tsetse-flies). Chapt. 5a (pp209-249) in K.G.V. Smith



- (Editor) Insects and Other Arthropods of Medical Importance. British Museum (Natural History), London xiv + 561pp + 12 plates.
- Riordan, K. 1968. Chromosomes of the tsetse fly, *Glossina palpalis* R.-D. Parasitology. 58:835-838.
- \_\_\_\_\_. 1970. Polytene chromosomes of *Glossina palpalis* Robineau-Desvoidy (Diptera: Muscidae). II. Their improved demonstration. Royal Entomological Society of London, Proceedings 45:184-186.
- Rogers, A. 1973a. Multiple mating by male *Glossina pallidipes* in the laboratory. Royal Society of Tropical Medicine and Hygiene (London), Transactions 67:298-299.
- \_\_\_\_\_. 1973b. A method for gauging the frequency of multiple mating of female *Glossina pallidipes* in the field. Royal Society of Tropical Medicine and Hygiene (London), Transactions 67:299.
- Rolseth, B.M. and R.H. Gooding. 1978. Genetics of *Glossina morsitans morsitans* (Diptera: Glossinidae) I. Electrophoretic banding patterns of xanthine oxidase and aldehyde oxidase. Canadian Entomologist 110:1233-1239.
- Service, M.W. 1978. A short history of early medical entomology. Journal of Medical Entomology 14:603-626.
- Shircore, J.O. 1913. On two varieties of *Glossina morsitans* from Nyasaland. Bulletin of Entomological Research 4:89.
- Southern, D.I. 1980. Chromosome diversity in tsetse flies. Chapt. 14 (pp225-243) in Blackman, R.L., G.M. Hewitt, and M. Ashburner (Editors). Insect Cytogenetics. Symposia of the Royal Entomological Society of London: Number Ten. Oxford, Blackwell Scientific Publications.
- \_\_\_\_\_, T.A. Craig-Cameron, P.E. Pell. 1972a. A critical chromosome analysis of *Glossina austeni* Newst. (Dipt., Glossinidae). Bulletin of Entomological Research 62:195-198.
- \_\_\_\_\_. 1972b. The meiotic sequence in *Glossina morsitans morsitans*. Royal Society of Tropical Medicine and Hygiene (London), Transactions 66:145-149.
- Southern, D.I. and P.E. Pell. 1973. Chromosome relationships and meiotic mechanisms of certain *morsitans* group tsetse flies and their hybrids. Chromosoma (Berl.) 44:319-334.
- \_\_\_\_\_. 1974. Comparative analysis of the polytene chromosomes of *Glossina austeni*, and *Glossina morsitans morsitans*. Chromosoma (Berl.) 47:213-226.
- \_\_\_\_\_. 1981. Cytogenetical aspects of *morsitans* tsetse flies with particular reference to *Glossina pallidipes* (Diptera, Glossinidae). Cytobios 30:135-152.
- \_\_\_\_\_, and T.A. Craig-Cameron. 1973a. Polytene chromosomes and cytological maps. Royal Society of Tropical Medicine and Hygiene (London), Transactions 67:304-305.
- \_\_\_\_\_. 1973b. An outline of sterility experiments conducted on sub-species of *Glossina morsitans*. Royal Society of Tropical Medicine and Hygiene (London), Transactions 67:305.
- \_\_\_\_\_. 1973c. Polytene chromosomes of the tsetse fly *Glossina morsitans morsitans*. Chromosoma (Berl.) 40:107-120.

- Southern, D.I., P.E. Pell, and P.A. Langley. 1975. The timing of pre-meiotic chromosome pairing and duplication in *Glossina morsitans morsitans* assessed by radiation induced mutations. *Cytobios* 12:179-189.
- Tobe, S.S. and P.A. Langley. 1978. Reproductive physiology of *Glossina*. *Annual Review of Entomology* 23:283-307.
- Vanderplank, F.L. 1944. Hybridization between *Glossina* species and suggested new method for control of certain species of tsetse. *Nature, London* 154:607-608.
- \_\_\_\_\_. 1947. Experiments in the hybridisation of tsetse-flies (*Glossina*, Diptera) and the possibility of a new method of control. *Royal Entomological Society of London, Transactions* 98:1-18.
- \_\_\_\_\_. 1948. Experiments in cross-breeding tsetse-flies (*Glossina* species). *Annals of Tropical Medicine and Parasitology* 42:131-152.
- \_\_\_\_\_. 1949. Variation in the male genitalia of the tsetse fly *Glossina pallidipes* (Austen) and a note on *G. austeni* (Newstead). *Royal Entomological Society of London, Proceedings (B)* 18:65-68.
- Vloedt A.M.V. van der 1980. Cross-breeding experiments with *Glossina morsitans morsitans* (Westwood) wild genotype and phenotype genetic marker *ocra*. in *Isotope and Radiation Research on Animal Diseases and Their Vectors*. International Atomic Energy Agency (Vienna) STI/PUB/525: 425-438.



Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English, and one in another language, preferably French.

Tables, including titles and footnotes, must not be more than 7 3/4 X 4 3/4 inches (19.7 X 12.1 cm). Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 3/4 X 5 inches, or 19.7 X 13.2 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, \$17.00 per volume of four issues, normally appearing at quarterly intervals; single issues \$5.00. Back volumes and issues are available at the same cost. There is a postal surcharge of \$4.00 to subscribers outside Canada. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to:

The Editor, *Quaestiones Entomologicae*  
Department of Entomology  
University of Alberta  
Edmonton, Alberta, Canada  
T6G 2E3

Quaestiones

Entomologicae

A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.

Publication of *Canadian Entomologist* was started in 1965 as part of a memorial project for Professor I. H. Strickland, the founder of the Department of Entomology at The University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printed charges. For information about current page charges, consult the Editor.

Style and preparation of papers should conform to the *Style Manual for Biological Journals*, published by the American Institute of Biological Sciences, second edition, 1964, except that titles of periodicals should be given in full. For style of reviewing papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English, and one in another language, preferably in French.

Copies for illustrations must accompany the manuscript, and be of such size as to permit satisfactory reproduction at page size (less 1.2 inch, or 1.2 cm). Plates of full page size (13.4 X 17.7 inches, or 19.7 X 13.2 cm). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, \$12.00 (U.S.) for subscribers within Canada, and \$17.00 (U.S.) for those outside Canada, per volume of four issues (single issues \$5.00). Back volumes are sold at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Correspondence regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

---

Published quarterly by

Department of Entomology  
University of Alberta  
Edmonton, Alberta, CANADA  
T6G 2E8

---

**Second Class Mail Registration Number 5222**

Change of address: inform mail to the address above. Return Postage Guaranteed

A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 20

Number 3

1984

CONTENTS

Ashe—Generic Revision of the Subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with Review of the Described Subgenera and Major Features of Evolution . . . . .	129
---	-----





**GENERIC REVISION OF THE SUBTRIBE GYROPHAENINA (COLEOPTERA:  
STAPHYLINIDAE: ALEOCHARINAE) WITH A REVIEW OF THE DESCRIBED  
SUBGENERA AND MAJOR FEATURES OF EVOLUTION**

*James S. Ashe*  
*Field Museum of Natural History*  
*Roosevelt Road at Lakeshore Drive*  
*Chicago, Illinois 60605*  
*U. S. A.*

*Quaestiones Entomologicae*  
20: 129-349 1984

**ABSTRACT**

*The world genera of the subtribe Gyrophaenina are revised and described; subgenera are reviewed.*

*Comparative morphological studies of adults reveal a great variety of characters available for taxonomic and phylogenetic study when gyrophaenines are examined in sufficient detail. Structures in the mouthparts, particularly the maxilla, proved especially useful. Illustrations of variation in structural features are provided.*

*Gyrophaenines are inhabitants of polypore and gilled mushrooms, where both larvae and adults feed by scraping maturing spores, basidia, cystidea and hyphae from the hymenium surface. Known features of natural history of gyrophaenines are reviewed. Many of these features are related to unusual features of mushrooms as habitats.*

*The subtribe is redefined, characterized, and larval characteristics are reviewed. The Gyrophaenina are shown to be monophyletic based on structure of the maxilla and spermatheca. Thirteen genera (11 previously described and two newly described) are recognized in the subtribe: Gyrophaena Mannerheim, Phanerota Casey, Eumicrota Casey, Encephalus Kirby, Probrachida n. gen. (type species Brachida modesta Sharp), Brachida Mulsant and Rey, Agaricochara Kraatz, Sternotropa Cameron, Pseudoligota Cameron, Neobrachida Cameron, Adelarhtra Cameron, Brachychara Sharp, and Agaricomorpha new genus (type species Gyrophaena (Agaricochara) apacheana SeEVERS).*

*Given for each genus are, as appropriate, synonymic list, diagnosis, description, discussion of nomenclatorial and taxonomic history, notes on natural history, general geographic distribution, and review of major literature.*

*Based on analysis of transformation series of 47 characters, a cladistic analysis of the genera is provided. Gyrophaenina is hypothesized to be sister group to the subtribe Bolitocharina. Within the Gyrophaenina, three lineages can be recognized, arbitrarily and informally designated the "Brachida", "Sternotropa" and "Gyrophaena" lineages. The "Brachida" lineage (Probrachida, Brachida) is hypothesized to be sister group to all other gyrophaenines, and the "Sternotropa" lineage (Sternotropa, Pseudoligota, Adelarhtra, Agaricomorpha, Brachychara, Neobrachida and probably Agaricochara) and the "Gyrophaena" lineage (Eumicrota, Gyrophaena, Phanerota) are hypothesized to be sister groups. Cladistic relationships of Encephalus cannot be determined at present.*

*Analysis of distribution of gyrophaenines among major types of host mushrooms compared with structural features in mouthparts and overlaid on a cladistic analysis of genera and analysis of major patterns of host relationships suggest hypotheses about major*

*features of evolution of gyrophaenines.*

At least two factors have had fundamental influence on evolution of relationships between gyrophaenines and mushrooms. First, evolution of mouthpart structures that allowed beetles to graze on the hymenium, rather than feed on fungal flesh, opened a relatively unused portion of the mushroom habitat. Second, general characteristics of the mushroom as a habitat require that members of each species evolutionarily optimize among conflicting requirements. These include: need to use every mushroom encountered, physiological limitations suggested by the great chemical and physical diversity of mushrooms, and physiological and competitive advantages expected from specialization. In resolving these conflicting requirements, gyrophaenines have evolved tolerance to a range of physical and chemical characteristics provided by mushrooms. This tolerance is reflected in an "acceptability spectrum" and allows members of a gyrophaenine species to respond to seasonal, yearly and geographic variation in the mushroom flora.

Major habitat types found among mushrooms, from ephemeral gilled mushrooms to persistent polypores, can be considered to provide a series of adaptive zones for gyrophaenines. Increasing reliance on hymenium scraping as a feeding mode is reflected in changes in structure of the maxilla. Life cycle adaptations to the ephemeral nature of gilled mushrooms was probably involved in attainment of this adaptive zone. This has occurred only among members of Gyrophaena and Phanerota. Other gyrophaenines appear to be restricted to polypores or habits are not known.

## RÉSUMÉ

L'auteur présente une révision générique de la faune mondiale de la sous-tribu des Gyrophaenina et passe en revue les sous-genres déjà décrits.

Une étude de morphologie comparée des adultes révèle un grand nombre de caractères utiles pour la taxonomie et la phylogénie lorsque les Gyrophaeninès sont examinés suffisamment en détail. Les structures les plus utiles sont celles des pièces buccales, particulièrement des maxilles. La variation des caractères structuraux est illustrée.

Les Gyrophaeninès habitent les polypores et les champignons à lamelles, dans lesquels larves et adultes se nourrissent en raclant les spores en maturation, les basides, les cystides et les hyphes se trouvant à la surface de l'hyménium. L'auteur revoit les aspects connus de l'histoire naturelle des Gyrophaeninès. Plusieurs de ces aspects sont reliés à des traits inusités de l'habitat que représentent les champignons.

La sous-tribu est redéfinie et caractérisée, et les caractéristiques des larves sont revues. La structure des maxilles et de la spermatheque indiquent que les Gyrophaenina forment un groupe monophylétique. L'auteur reconnaît 13 genres dans la sous-tribu (11 décrits antérieurement et deux nouvellement décrits): Gyrophaena *Mannerheim*, Phanerota *Casey*, Eumicrota *Casey*, Encephalus *Kirby*, Probrachida *n. gen.* (génotype *Brachida modesta Sharp*), *Brachida Mulsant et Rey*, *Agaricochara Kraatz*, *Sternotropa Cameron*, *Pseudoligota Cameron*, *Neobrachida Cameron*, *Adelarthra Cameron*, *Brachychara Sharp*, et *Agaricomorpha n. gen.* (génotype *Gyrophaena (Agaricochara) apacheana Seever*).

Les items suivants sont présentés pour chaque genre, lorsqu'appropriés: liste des synonymes, diagnose, description, discussion de l'histoire nomenclatoriale et taxonomique, notes sur l'histoire naturelle, grandes lignes de la répartition géographique et revue de la littérature principale.

L'étude des séries de transformations de 47 caractères a servi de base à une analyse cladistique. L'hypothèse est émise à l'effet que les Gyrophaenina forment le taxon frère de la sous-tribu des Bolitocharina. Parmi les Gyrophaenina, trois lignées se distinguent et sont désignées de façon arbitraire et informelle sous les noms de "Brachida", "Sternotropa" et "Gyrophaena". La lignée "Brachida" (comprenant les genres *Probrachida* et *Brachida*) formerait le taxon frère de tous les autres Gyrophaeninès, et les lignées, "Sternotropa" (incluant *Sternotropa*, *Pseudoligota*, *Adelarthra*, *Agaricomorpha*, *Brachychara*, *Neobrachida* et probablement *Agaricochara*) et "Gyrophaena" (comprenant *Eumicrota*, *Gyrophaena* et *Phanerota*) seraient taxons frères. Il n'est présentement pas possible d'établir les relations cladistiques d'*Encephalus*.

La distribution des Gyrophaeninès parmi les principaux types de champignons-hôtes est comparée avec les caractéristiques structurales des pièces buccales. Cette comparaison est superposée à une analyse cladistique des genres ainsi qu'à une analyse des principaux types de relations avec les hôtes, ce qui permet de formuler des hypothèses sur les principaux aspects de l'évolution des Gyrophaeninès.

Au moins deux facteurs ont eu une influence fondamentale sur l'évolution des relations entre les Gyrophaeninès et les champignons. Premièrement l'évolution de structures particulières des pièces buccales, qui permet à ces Coléoptères de

*brouter sur l'hyménium plutôt que de consommer la chair des champignons, a rendu possible l'exploitation d'une portion relativement inutilisée de l'habitat constitué par les champignons. Deuxièmement, les caractéristiques générales des champignons en tant qu'habitat requièrent que les membres de chaque espèce de Gyrophaeninés soient adaptés pour satisfaire optimalement à des exigences incompatibles. Ces exigences comprennent: la nécessité d'utiliser chaque champignon rencontré, les limitations physiologiques que suggère la grande diversité physique et chimique des champignons, et les avantages physiologiques et compétitifs découlant de la spécialisation. Pour répondre à ces exigences incompatibles, les Gyrophaeninés ont évolué une tolérance à une gamme de caractéristiques physiques et chimiques des champignons. Cette tolérance est reflétée par la variété des champignons acceptables et permet aux membres des Gyrophaeninés de suivre les variations saisonnières, annuelles et géographiques de la flore mycologique.*

*Les principaux types d'habitats offerts par les champignons, allant des espèces à lamelles éphémères jusqu'aux polypores persistants, peuvent être perçus en termes d'une série de zones adaptives pour les Gyrophaeninés. Des changements dans la structure des maxilles reflètent une dépendance accrue du broutage de l'hyménium comme mode de nutrition. L'accès à cette zone adaptive impliqua probablement l'ajustement des cycles vitaux à la nature éphémère des champignons à lamelles. Cette adaptation n'a évolué que chez les membres de Gyrophaena et de Phanerotia. Les autres Gyrophaeninés dont le mode de vie est connue semblent n'utiliser que les polypores.*

## TABLE OF CONTENTS

Introduction	132
General Introduction to the Gyrophaenina	132
Objectives of this Study	133
Materials and Methods	133
Materials	133
Methods	133
Structural Features of Gyrophaenina	140
Introduction	140
General Characteristics	142
Detailed Characteristics	143
Natural History of Gyrophaenina	222
Habitat	222
Life History	224
Interactions with other mushroom-inhabiting insects	231
Perspectives on Classification	232
Taxa of Gyrophaenines Examined	233
Description and Reclassification of World Genera of Gyrophaenina	236
Identification of the World Genera of Gyrophaenina	239
Genera and subgenera of Gyrophaenina	242
Evolutionary Analysis of Genera of Gyrophaenina	265
Character Analysis	265
Phylogenetic Analysis	290
Evolutionary Trends in Gyrophaenina	312
Introduction and Methods	312
Mushrooms as Habitats	314
Adaptations to the Mushroom Habitat	317
Patterns of Host-Mushroom Relationships	323
Adaptive Zones and Possible Evolutionary Scenarios	333
Prospectus: Future Trends in Research within the Gyrophaenina	335
Acknowledgements	336
Literature Cited	337
Index to Names of Insect Taxa and Host Plants	346

## INTRODUCTION

## General Introduction to the Gyrophaenina

The Gyrophaenina are a subtribe of beetles in the huge, very incompletely known staphylinid subfamily Aleocharinae. As recognized in this revision, the subtribe is composed of 13 genera, within which have been described more than 500 species. This appears to be only a small portion of the extant species. More than 100 species occur in the relatively well known fauna of America north of Mexico alone, and about 20% of these are undescribed. Gyrophaenine faunas of tropical areas are inadequately known, and experience indicates that the group is very diverse there. Most described species have been placed in the heterogeneous genus *Gyrophaena* Mannerheim.

Most gyrophaenines are rather parallel-sided and more or less dorso-ventrally depressed. However, body forms are varied, including markedly robust (members of *Encephalus* Kirby) and sub-limuloid forms (members of *Brachychara* Sharp). Generally, gyrophaenines are small to very small beetles. Size of adults is from over 3.0 mm to only 0.6 mm in length. Most are between 1.2 and 2.3 mm long.

Members of Gyrophaenina are obligate inhabitants of fresh mushrooms as larvae and adults. They live on both polypore and gilled mushrooms. Adults appear on mushrooms soon after the gills are exposed or the hymenium area becomes active, and both larvae and adults occupy more mature mushrooms. Gyrophaenines inhabit only fresh mushrooms and are usually among the first insects to appear on them.

A wide variety of staphylinids live on mushrooms. Most, however, are probably predaceous on other organisms which occur there, or, at most, are facultatively mycophagous. Gyrophaenines are unusual among staphylinids in that they are exclusively mycophagous as both larvae and adults. Additionally, gyrophaenines are unusual among mycophagous insects in that they are adapted to feed on the active spore-producing layer of mushrooms, in contrast to the more usual habit of burrowing into the flesh.

Gyrophaenines can be both abundant and locally diverse. I have collected more than 700 adults representing 13 species from a single fruiting body of *Amanita verna* (Lam. ex Fr.). While such large numbers of individuals per mushroom are exceptional, it is not unusual to collect tens of individuals per fruiting body. Hundreds of gyrophaenines can usually be collected on a brief collecting excursion whenever mushrooms are common. In addition, local diversity may be very high. Within a single small woodlot in the Blue Ridge Mountains of North Carolina, I have collected 35 species in a single season.

The subtribe Gyrophaenina has not been clearly delimited or described in detail. For this reason, the genera which have been assigned to the subtribe comprise a very heterogeneous assemblage. Genera have not been adequately described and illustrations of structural features have usually not been provided. All of this has resulted in confusion about generic limits and assignments.

When I became interested in host relationships of gyrophaenines in collaboration with J.F. Cornell, it soon became apparent that little understanding of evolution of host relationships could be developed until the systematics of the group was more clearly understood. Therefore, when opportunity arose, this study was initiated.

### Objectives of this Study

In this study, I treat in detail the systematics and evolution of the genera of the subtribe Gyrophaenina and review the described subgenera. I demonstrate that the Gyrophaenina form a monophyletic group and assign appropriate genera to it. I describe in detail and provide keys for identification of all genera. I provide a detailed discussion of known character systems and provide analysis of polarity of transformation series. Using this information, I develop initial hypotheses about cladistic relationships among gyrophaenine genera. Finally, by superimposing known natural history information, in particular host relationships, on cladistic analysis, I make first hypotheses about major features in evolution of gyrophaenines and how characteristics of mushrooms as habitats have affected patterns and processes of evolution of gyrophaenines.

This revision is intended to provide a base and stimulus for further research on gyrophaenines. I suspect many of the systematic and evolutionary conclusions reached here will require modification after the group becomes better known.

This revision is not primarily a study of host relationships and natural history of gyrophaenines. However, an understanding of gyrophaenine evolution requires consideration of natural history and host relationships. Within the limitations of this study, the treatment of host relationships cannot be exhaustive. General features of host relationships are discussed and initial hypotheses about origin and nature of host relationships are developed. I hope this discussion will stimulate more detailed studies of host relationships and evolution of this particularly interesting group of beetles.

## MATERIALS AND METHODS

### Materials

This revision is based on examination of more than 15,000 adult specimens of more than 350 described and many undescribed species. Specimens representing all genera and primary type material of type species of most genera included in this treatment were examined. In addition, for comparative information, specimens of both closely and more distantly related aleocharines were examined in detail.

I have collected gyrophaenines throughout America north of Mexico, particularly in the Southeast, Southwest and Gulf States, and in Mexico and much of Canada. I have examined type material, and specimens of described and undescribed gyrophaenines from all geographic regions during visits to the British Museum (Natural History), Canadian National Collection, Field Museum of Natural History, and United States National Museum. I have received on loan type and non-type material from the British Museum (Natural History), Field Museum of Natural History, Museum of Comparative Zoology, and the personal collections of J.F. Cornell and J.H. Frank. Of particular note is a very excellent collection of Mexican and Central American gyrophaenines loaned to me by A.F. Newton of the Museum of Comparative Zoology. I have received gifts of Central and South American gyrophaenines from H. Frania and South American gyrophaenines from Ian Moore.

### Methods

*Collection and Preservation of Specimens.*— The most convenient method of collecting gyrophaenines from mushrooms is simply to remove a mushroom from the substrate and shake it sharply over a white enameled pan. Adult gyrophaenines will fall from the mushroom and may be aspirated and transferred to preserving medium. Many larvae cling to the mushroom and must be searched for between the gills or on the pore surface or in cracks and crevices of

polypore mushrooms. Larvae may also be removed from the fruiting body by dropping the entire mushroom into 70% alcohol. Larvae will quickly leave the mushroom. Because of the large quantity of alcohol required, the method is seldom practical except for very small fruiting bodies.

Many adults and larvae of species which occur on polypores, particularly resupinate polypores on logs, take refuge in cracks and crevices at the base of the fruiting body or under flakes of bark near the mushroom. These areas should be examined for gyrophaenines.

Occasionally gyrophaenines may be collected from leaf litter or under logs, especially at times when mushrooms are uncommon. However, this is not a reliable way to collect gyrophaenines, although members of some species (e.g., *Encephalus* spp., *Probrachida* spp. and *Brachida* spp.) are apparently most commonly collected in moldy litter.

Gyrophaenines are diurnal and therefore only a few adults are found in light trap samples.

It is wise to collect large series of gyrophaenines — in particular, all the individuals found on a mushroom or group of mushrooms. Many samples yield a few specimens of rare or uncommonly collected species mixed with a large number of a more common species. Also, in many samples, a number of species are represented among the specimens from a single mushroom, although members of one species predominate.

There are two reasons for keeping specimens collected from each species of mushroom separate. First, in practical terms, this greatly facilitates sorting. Because of the host affinities of gyrophaenines, the number of similar species which must be distinguished within such a mixed series is greatly reduced in comparison to a mixed series from all available mushrooms in an area. A mixture of gyrophaenines from all mushrooms encountered on a collecting trip may contain 20 or more species, many represented by a large number of individuals, and many of them very similar in external structure. Sorting such a mixture can be very arduous. In particular, association of females with males is very uncertain in many samples. Second, only material in which individuals from each species of mushroom are kept separate can supply data about host associations.

Study of host relationships of gyrophaenines is of particular interest, and host information should always be collected. Specimens with host identified to species are most valuable. Although confident identification of most mushrooms is very difficult for the non-specialist, this should not deter a collector from recording whatever information can be obtained under the circumstances. Host identification to genus can be very useful. Even such information as “ex brown-spored gilled mushroom”, “ex fleshy polypore”, or “ex gilled mushroom on log” is useful at some levels of analysis.

In studies of host relationships of gyrophaenines, all specimens encountered on a particular mushroom or group of mushrooms of the same species should be collected. Not only may a number of species be encountered on a particular mushroom, but relative number of individuals of each gyrophaenine species is also of prime importance.

It is desirable to make a voucher collection of mushrooms from which gyrophaenines are collected. Such a voucher collection is almost essential for serious and detailed studies of host relationships of gyrophaenines. Methods and equipment required for collecting mushrooms are described in a number of popular and semi-popular books about mushrooms (e.g., Smith and Smith, 1973; Krieger, 1967).

Collection of information to answer more detailed and specific questions about host relationships requires more meticulous and complex methods of sampling and handling of material and host information.

Gyrophaenines are best killed and preserved in 70% ethanol with a few drops of acetic acid added to each vial. The problem of hardening of specimens killed in alcohol is somewhat alleviated by the acetic acid.

Despite the inconvenience of hardened specimens, collection and storage in fluid has a number of advantages. Sorting of mixed collections of these small beetles is greatly facilitated. Manipulation of specimens to view diagnostic characters and direct comparison of similar specimens is much easier in fluid than with dried specimens. The optical properties of fluid make it much easier to distinguish subtle differences in punctuation, sculpture and proportion which are obscured by reflections, distortion or setation in dried specimens. Many gyrophaenines have quite thin integuments which are subject to distortion upon drying. Proportions and diagnostic characters of many dried specimens are obscured or altered, making identification of a mixed series difficult. Storage in fluid allows one to conveniently keep and maintain long series of gyrophaenines. If a traditional collection of dried specimens is desired, a few specimens of each series may be mounted on points or cards.

Gyrophaenines are small, rather delicate-bodied insects, and collection into typical sawdust tubes with ethyl acetate results in many distorted or damaged specimens, especially if they are not removed promptly. Damage can be eliminated to some extent by using filter paper rather than sawdust as an absorbent medium.

A long series of gyrophaenines should not be stored dry in gelatin capsules as is done by some workers. Damage to specimens under these conditions is virtually assured even if they are packed carefully.

*Dissection Techniques.*— Confident identification of gyrophaenines requires examination of male genital capsules. This requires digestion or maceration of the muscles around the genital capsule and subsequent dissection of the beetle for removal of this capsule.

Dried material should first be softened by washing in warm distilled water, then transferred to cold 10% potassium hydroxide (KOH) for clearing. Fluid preserved material should be handled similarly after being first rinsed in distilled water. After an entire beetle has been cleared in 10% KOH for one to three hours, depending on size, it should be washed several times in distilled water then transferred to distilled water for dissection.

It is most convenient to remove the aedeagus from inside the abdomen. This is easily done by inserting a fine needle into the membrane between abdominal segments 6 and 7. Teasing of this membrane allows separation of abdominal segments 7 to 10 with the enclosed genital capsule from the remainder of the abdomen. The genital capsule can now be removed through the proximal end of abdominal segment 7 with the aid of a very fine needle with a small hook at the tip and a pair of fine forceps.

One or both parameres should be removed from the genital capsule to provide a clear view of the lateral aspect of the median lobe.

With fresh material or material which is suitably soft, it is possible to dissect the genital capsule without clearing the entire beetle in KOH. Under these circumstances, identification is greatly speeded and one avoids the danger of clearing and subsequent distortion of a valuable specimen. However, because of strong muscles between the abdominal segments and muscles associated with the genitalia, damage to the beetle and aedeagus is more likely under these conditions. Therefore, dissection of uncleared material should be avoided except under special circumstances.

An alternative procedure is to remove the apical abdominal segments from specimens softened in distilled water as described above, and transfer these with the included genital

capsule to KOH for clearing. Again, however, attempting to remove abdominal segments from uncleared material commonly results in considerable damage to the abdomen. This should be avoided if possible. As pointed out by Seevers (1951), it is a good practice to habitually place one or several males from each series into KOH for clearing.

Because most aleocharines are small, detailed study of character systems requires specialized handling. A multitude of character systems is available for analysis when these small beetles are examined in adequate detail.

The procedure I use for preparation of a specimen for detailed examination is the following.

- 1) Wash and sonicate the specimen thoroughly in distilled water to which a few drops of a mild liquid detergent have been added. Remove the soapy residue by washing in distilled water.
- 2) Clear the specimen three to five hours in cold concentrated KOH. Cold KOH, while slower, seems to cause less deformation than hot KOH.
- 3) Wash in several changes of distilled water to which a few drops of acetic acid have been added. Subsequent handling of the specimen is determined by the examination method anticipated. If one is planning to make permanent slide mounts for study, the specimen may now be transferred to 70% ethanol for dissection.
- 4) For reasons stated below, I prefer to examine specimens in glycerine. Transfer to glycerine must be made with care to avoid distortion of the specimen. I prefer to transfer the specimen to a mixture of 4% glycerine in 10% ethanol-distilled water. For very delicate specimens it is helpful to first make small pinpricks in the membrane behind the head, at the base of the metathorax, and near the tip of the abdomen.

The specimen should be transferred to the 4% glycerine solution in a wide-mouthed container such as a watch glass. The glycerine is concentrated by allowing water and ethanol to evaporate from the solution at room temperature, with addition of 4% glycerine as the fluid level drops. After two or three such additions the solution is allowed to evaporate as far as possible. The specimen is now ready to be transferred to concentrated glycerine on a depression slide for dissection.

Several fine minute pins mounted on thin wooden handles plus one or more pairs of very fine pointed forceps are useful for careful dissection of these small insects.

The mouthparts should be removed for examination. This is best effected by inserting a fine needle laterally beneath the mentum through the membrane at the base of the maxillary cardo. Pressure on this point results in separation of the labium, and often one or both maxillae, from the head capsule. This exposes the bases of the mandibles and labrum for easy subsequent removal.

Abdominal segments 7 to 10 should be separated from the remainder of the abdomen as described above, and the genital capsule of males or spermatheca of females removed.

Additional dissection depends on the needs of the investigator. Removal of legs, antennae, wings and separation of the major body regions is often useful.

Because genital capsules of gyrophaenines have relatively uniform internal structure, dissections of this structure were not performed in this investigation. However, in many groups of aleocharines, internal structure of the aedeagus is very complex and study of these character systems would probably prove rewarding. Sawada (1972) offers techniques for dissection and study of internal structure of the genital capsule.

*Detailed Examination.*— Detailed examination of the specimen plus dissected parts is conveniently done in a drop of glycerine on a depression slide at magnifications ranging from 100 to 400X (depending on working distance of the objective lens). Working with material in glycerine rather than on prepared and permanent slides has a number of advantages. Because



of the complex three-dimensional structure of many of the parts examined, and the very low depth of field at high magnifications, complex structures may be difficult to interpret in light microscopy. Materials in glycerine mounts are easily oriented to view other aspects of the same structure, providing additional information about the relationships of the structural components. It also allows reorientation to observe the widest possible range of characters in the same specimen.

Dissected material in glycerine is conveniently stored in glycerine in microvials pinned through the cork and handled as regular pinned material. Structural components are easily extracted from the microvial and placed in a drop of glycerine for re-examination or observation of a newly discovered character system. Also, dissected material stored in glycerine in microvials requires no specialized storage techniques, and is less likely to be separated from the main body of a collection or misplaced, as happens with many permanent slide mounts.

I prefer to place the main body of the specimen in one microvial, and all dissected components in another, pinned beneath it. This greatly facilitates relocation of any required parts. All parts removed from gyrophaenines should be stored in transparent glass microvials rather than the semitransparent plastic microvials used by many workers. Many dissected parts of gyrophaenines are less than 0.1 mm in length, and must be located within the microvial under magnification before they can be removed for examination. Semitransparent vials preclude this and parts may be lost.

Examination of very small structures such as structure and position of sensilla requires higher magnifications (often oil immersion) than is possible with glycerine mounts, because of the very short working distances of very high magnification objectives. Material mounted on permanent slides is best for examination of these character systems.

Subsequent storage depends on the original source, degree of dissection, and future deposition of the specimen. The body of a beetle may be mounted on a card or point and dissected parts in a microvial pinned beneath the beetle. Both beetle and dissected parts may be placed in glycerine in microvials pinned through the cork, or mounted on a permanent slide, or transferred to alcohol and stored with the remainder of the series of the same species.

Mounting a genital capsule dry in a drop of glue should be avoided. Because of the small size and thin integument of these structures, unacceptable distortion occurs on drying.

Gyrophaenines in particular and aleocharines in general are ideal subjects for examination with the scanning electron microscope. Though small, they are amazingly complex in detailed structure, especially mouthparts. Under these circumstances, the unique capabilities of the SEM are displayed to the best advantage. However, I recommend that time be taken to become thoroughly familiar with the fine structure of a beetle using light transmission microscopy before going to the SEM. This reduces the probability that SEM photomicrographs will be used to illustrate diagnostic features which are more clearly illustrated by a drawing. This also avoids confusion in orientation at magnifications possible with the SEM and allows more productive use of expensive SEM time.

*Sex Determination.*— Males of most gyrophaenine species display secondary sexual characteristics — particularly on tergum 8 — while females of most species lack such modifications. Therefore, for most species, examination of a specimen for secondary sexual modifications is sufficient to determine its sex. However, both sexes of a few species have strikingly different secondary sexual modifications, while specimens of both sexes of other species lack external modifications.

Male gyrophaenines, and males of all other aleocharines, are recognized by presence of a tenth sternum which is lacking from females. Sternum 10 is difficult to see in many dried specimens because of telescoping of the abdomen or distortion on drying. However, presence or absence of this sternite remains the only means of distinguishing sexes by external examination of those species in which secondary sexual characteristics are lacking or similar in both sexes.

*Measurements.*— Standardization of measurements is important for study of any group, particularly so for study of aleocharines, because body proportions are useful as both taxonomic and phylogenetic characters.

Staphylinids in general, and aleocharines in particular, offer a number of problems for accurate measurement. Thin integument and flexible body of many staphylinids result in distortion upon drying, telescoping of the abdomen, and flexure of body parts into unusual positions.

It is important that a part being measured be oriented so that it is as flat in the plane of the measuring device as possible. Also, specimens should be chosen which show as little distortion due to collecting, preservation or preparation processes as possible. Accuracy of measurement is vital. Depending on subtlety of differences measured, and size of parts in relation to accuracy of the measurement apparatus, differences can be masked or falsely implied by mismeasurement by the width of a grid or reticule line. This source of error makes it difficult to quantify, for example, small differences in relative lengths and widths of antennomeres which are distinguishable visually.

To reduce this error, the most extreme edge of a structure being measured should be oriented so that it appears just in contact with the inner edge of the measuring line. This seems to be a less ambiguous position for measurement than trying to orient the edge of the structure to the middle of the measurement line. Extrapolations between measurement lines should be made as accurately as possible.

Measurements and ratios used in this study are described and justified below.

1. Total Length (T.L.) — Total length has typically been one of the most ambiguous and difficult of major measurements of the adult staphylinid body, because of relative mobility of the body. The head, prothorax, and particularly the abdomen may be flexed into quite different planes, or segments may be telescoped into one another — a particular problem for abdominal segments of dried specimens. Various conventions for making unambiguous measurements have been suggested. In this study, I use distance from anterior margin of the labrum to apex of abdomen. The most useful range is that suggested by Herman (1972), and is taken by measuring the shortest and most contracted specimen, and the longest and most distended specimen.
2. Head Length (H.L.) — Head length is measured along the midline from the most anterior margin of the clypeus to base of head, not including the slightly sclerotized broadly triangular area at the base of the head.
3. Head Width (H.W.) — This is the greatest width at the point at which the tempora contact the posterior margin of the eye. This differs from traditional measurements of head width in that it does not include the eyes. This measurement provides a more meaningful comparison to head length than the more inclusive measurement.
4. Head Width to Length Ratio (H.W.:H.L.) — This ratio provides a measurement of the relative transversality of the head.
5. Eye Size (E.S.) — Eye size is expressed as a ratio of total length of eye from its anterior to posterior margin compared to total head length. This ratio measures amount of lateral

margin of the head which is occupied by the eyes, and is explained more fully in the appropriate section of the discussion of structural features. An alternative measure of eye size, not used here, is greatest width of head including eyes compared to the interocular distance. This is an indication of relative protrusion of the eyes.

6. Pronotum Width (P.W.) — Greatest width in dorsal aspect.
7. Pronotum Length (P.L.) — Length of pronotum from anterior margin to posterior margin along midline. For specimens with posterior margin of pronotum incised medially, the length is distance from anterior margin to an imaginary line tangent to the most posterior points on the posterior margin.
8. Pronotum Width to Length Ratio (P.W.:P.L.) — This ratio reflects relative transversality of the pronotum.
9. Elytra Length (E.L.) — Distance along suture from posterior margin of scutellum to an imaginary line tangent to posterior margins of elytra. (Construction of this line is necessary because, in some specimens, the lateral angle is more posterior than the sutural angle of the elytron.)
10. Elytra Width (E.W.) — Greatest transverse distance across both elytra when in normal repose.
11. Elytra Width to Length Ratio (E.W.:E.L.) — This ratio describes the relative transversality of the elytra.
12. Elytra Length to Pronotum Length Ratio (E.L.:P.L.) — This ratio is very useful descriptively since it compares the relationship between lengths of two structures which contribute markedly to the overall habitus of the beetle.
13. Mesosternal Process to Isthmus to Metasternal Process Ratio (Ms.P.:I:Mt.P) — As discussed most recently by Seevers (1978) (see also appropriate section under structural features), there are well defined meso- and metasternal processes extending between the mesocoxae. Length of the mesosternal process is measured from an imaginary transverse line tangent to anterior margins of mesocoxae to the most posterior apex of the process. The length of the metasternal process is measured from an imaginary transverse line tangent to the posterior margins of the mesocoxae to the most anterior apex of the process.

In many aleocharines, these processes do not meet, and are separated by an anterior extension of the metasternum dorsal to the metasternal process, called the "isthmus". In gyrophaenines, the meso- and metasternal processes meet, and length of the isthmus is thus 0. Therefore, description of the intercoxal structures will be given as the ratio "length of mesosternal process to length of metasternal process" (Ms.P.:Mt.P.).

*Illustrations.*— Line drawings of structural features were made with the aid of a drawing tube, with Varimag Zoom attachment, on a Wild M-20 compound microscope, at magnifications from 50 to 650 diameters depending on the structure and detail required. Scale lines are included although relative sizes of structures are not here considered taxonomically or phylogenetically important characters. Drawings were compared to the structure after inking to verify accuracy.

Scanning electron micrographs were made with two different instruments. Figures 238–244 were obtained with a Cambridge S-4 Stereoscan SEM, while Figures 233–237 and 245–250 were made with a Cambridge Stereoscan 250.

Illustrations are arranged in the following order within the text: 1) drawings of structural features illustrating states of taxonomically or phylogenetically important characters; 2) diagrams and figures referred to in discussions of phylogenetic analysis; and 3) diagrams and

figures referred to in discussion of evolutionary trends.

Distribution maps are not provided since this revision is concerned only with superspecific taxa. Instead, distributions are given in the text.

*Descriptive Format.*— Each description of a generic-level taxon provides reference to the original publication of the valid name of the taxon in the form in which it was first published, and the original publication of each junior synonym in its original form.

A diagnosis of each genus is given, which provides more information than the key about useful recognition characteristics. Generic determinations based on the key should be verified by reference to the diagnosis.

Following the generic description, a brief survey of the nomenclatorial and taxonomic history of the genus is provided. This is followed by a discussion of important characters for delimitation and limits of the genus. Where appropriate, a discussion of important or particularly complex structural variation is provided, along with a suggestion of character systems likely to be useful for species recognition and diagnosis, and character systems expected to be useful for phylogenetic analysis of species or species-group assemblages within the genus.

A brief review of the general natural history (*e.g.*, habits and general host trends) of each genus is provided whenever such information is available. References to major literature discussing natural history or habits of members of each genus are given, followed by references to any descriptions or information about immature stages of members of that genus.

General distribution of members of the genus and major descriptive and revisionary literature is reviewed.

Though I have examined specimens (often type material) of about 80% of the described species of gyrophaenines, because of the large number of described species, the amount of synonymy and homonymy involved, difficulty of making accurate generic assignments based on superficial examination, and the systematic work needed within the heterogeneous group of species now included in *Gyrophaena*, it is premature to attempt a detailed reassignment of species to appropriate genera. I have, therefore, included only lists of described species placed in new combination under newly described genera. Lists of described species of gyrophaenines are available in a variety of catalogues such as Fenyés (1918-21), Bernhauer and Scheerpeltz (1926), Scheerpeltz (1934), Blackwelder (1943), Seevers (1978), appropriate parts of Zoological Record, and major literature discussed under each generic discussion.

## STRUCTURAL FEATURES OF GYROPHAENINA

### Introduction

Character systems on which most taxonomic research within the Aleocharinae have been based were essentially established by Erichson (1839-40) and were later extended and more firmly entrenched by Ganglbauer (1895). Since these important studies, taxonomic research among higher taxa within the Aleocharinae has been based on number of articles of the tarsi, maxillary palpi, labial palpi and antennae of adult beetles. Many of these structures are small and difficult to see in dried specimens. Many characters previously used diagnostically at lower taxonomic levels are qualitative and difficult to describe accurately, or they vary in unexpected and undescribed ways. Also, almost all studies suffer from lack of adequate illustrations.

Few character systems generally used for systematic research within the Aleocharinae have been studied comparatively. Thus, extent of variation in character systems, and implications of that variation for taxonomic reliability and phylogenetic analysis are unknown or, at best,

inadequately understood.

This lack of detailed comparative structural studies within the aleocharines, coupled with the small size of most adults and large number of valid taxa, has combined to make this the most inadequately understood large group within the Coleoptera. In fact, the complexity of the group and small size of its members have left many taxonomists with the impression that members of the Aleocharinae as a whole exhibit a basic uniformity of structure and lack character systems suitable for serious analytical study. Even Lars Brundin, after several excellent studies on athetine aleocharines, abandoned the group for study of the Chironomidae because of presumed lack and limited understanding of character systems (Brundin, 1972, p. 72). Much of this erroneous opinion has resulted from use of traditional equipment and techniques. Examination of aleocharines using techniques more suited to their small size (see above), yields a great variety of structural features for comparative morphological study at all taxonomic levels.

The first major, though limited, attempt at a general comparative description of members of the Aleocharinae was provided by Fenyès (1918-21) in the introduction to his monograph on the aleocharine genera of the world.

Detailed comparative structural analyses were provided by Brundin (1942, 1943, 1945, 1952, 1954) for general characteristics of several athetine groups, with particularly comprehensive discussions of characters available on the male copulatory organs. Hoeg (1945) discussed variation and taxonomic usefulness of distribution of setae and bristles on the thorax of adult athetine aleocharines. However, the precedent set by the comprehensive discussions of Brundin and Hoeg has been followed by few subsequent workers.

Recently, a number of workers has begun to recognize advantages provided by more detailed study of comparative morphology within the aleocharines. Two monographs by Seevers (1957, 1965) about termitophilous and myrmecophilous staphylinids, the majority of which are aleocharines, stand out among their contemporary papers by virtue of analysis of structural variation in the included groups, and the more convincing taxonomic and phylogenetic conclusions these analyses allowed. Hammond (1975) discussed a number of seldom used character systems in classification and phylogenetic analysis of the aleocharine tribes Gymnusini and Deinopsini. Seevers (1978) provides a general discussion of systems useful for characterization of genera and tribes. Seevers concentrated on characteristics of male genitalia, and gave a far less comprehensive discussion of variation in such important character systems as mouthparts, although he recognized the importance of these structures (p. 24).

Of particular importance in comparative study within the Aleocharinae are recent works by Sawada (1970, 1972). These studies, in addition to providing a comprehensive analysis of general structural variation among aleocharines, are the first attempts to provide a firm base for comparative study of the large number of useful structural characters found in the mouthparts of aleocharines. Character systems discussed in Sawada's papers have been used effectively in studies of the difficult athetine complex of genera and species by Sawada (1974, 1977) and Yosii and Sawada (1976).

In this section I introduce structural features of members of the subtribe Gyrophaenina, provide a general discussion of how these features vary within the group, and point out the extensive variety of structural features available for comparative study of gyrophaenines.

The studies mentioned above, especially those of Sawada, along with my own comparative morphological research within the aleocharines, form the basis for this discussion.

### General Characteristics

The wide variety of basic habitus types found within the Gyrophaenina makes it difficult to give a general description of a gyrophaenine. Body builds range from very robust (specimens of *Brachychara* and *Encephalus*) to slender elongate (*Gyrophaena* (*Phaenogyra*) *gracilis* (Seevers)); broadly oval in outline (specimens of *Encephalus*), to parallel-sided (many species of *Gyrophaena*, *Phanerota*, *Eumicrota* and others), to sublimuloid (specimens of some *Sternotropa*, *Brachychara*, *Adelarthra* and some *Pseudoligota*); and dorso-ventrally flattened (most *Gyrophaena* and others) to broadly oval in cross section (specimens of most robust species).

The basic body outline of most specimens is reflected in proportions of the anterior part of the body. Species in which members are parallel-sided to elongate have moderately transverse to subquadrate pronota. In contrast, specimens of species which are more or less limuloid have a moderately to markedly transverse head and pronotum, associated with a relatively wide elytral base. The effect is to make them look relatively "broad-shouldered". In specimens of most of these sublimuloid species, the abdomen tapers uniformly from the base of the elytra to the apex of the abdomen.

In general vestiture, the body varies from uniformly covered with short microsetae (e.g., many species of *Sternotropa*), to microsetae moderately reduced (e.g., many species of *Gyrophaena*), to nearly bare of microsetae (e.g., *Adelarthra*). The general appearance of some species is very much affected by enlargement of some macrosetae on the thorax, elytra and/or abdomen (as in specimens of *Adelarthra barbari*). Conversely, macrosetae of some species are very small and virtually impossible to distinguish from microsetae, except in slide preparations (e.g., some *Sternotropa*, *Pseudoligota*, and *Agaricomorpha*).

The eyes are very large and prominent in members of *Phanerota*. No species of gyrophaenine have substantially reduced or absent eyes.

Antennae are very long (as long as the head, pronotum and elytra together), with antennomeres 5-10 elongate (e.g., members of the *Gyrophaena pulchella* species group) to quite short (only slightly longer than the head and pronotum together) with antennomeres 5-10 transverse (e.g., members of most species of *Eumicrota*).

Body color shows considerable variation within the gyrophaenines. Members of most species associated with polypores tend to be uniformly dark brown, piceous or black (e.g., *Agaricomorpha*, *Eumicrota*, *Sternotropa* and *Pseudoligota*). Gyrophaenines associated with gilled fungi vary considerably more in color, from uniformly dark (*Gyrophaena wisconsinica* (Seevers)), to uniformly light (*Gyrophaena compacta* Seevers). Contrasting colors are relatively common. A striking example of color contrast is exhibited by specimens of *Phanerota fasciata* (Say), in which rufo-flavate ground color contrasts with black head, black outer apical third of elytra, and darkly clouded abdominal terga 6 and 7. Members of numerous other species exhibit similar, though less markedly contrasting, color patterns.

Size also differs considerably among species. Members of one of the largest species, *Gyrophaena vitrina* Casey, reach a length of 3.5 mm. In contrast, members of some undescribed species of neotropical *Eumicrota* are as small as 0.6 mm. Adults of many species of *Eumicrota*, *Pseudoligota* and *Gyrophaena* are 1.0 mm or less in length. These small gyrophaenines are among the smallest beetles known (exclusive of many ptiliid adults). Specimens of the majority of species of gyrophaenines are between 1.2 and 2.3 mm in length.

### Detailed Characteristics

**Microsculpture.**— The most common microsculpture among gyrophaenines is an isodiametric mesh with polygonal sections of cuticle delimited by sharply defined channels between the polygons. The most frequent modification of this basic pattern is a shallowing of channels so that the polygon edges are indistinctly delimited. Continuation of this trend results in complete loss of the channels between the polygons producing a smooth, strongly shining cuticular surface.

Cuticular areas exhibiting these types of microsculpture are termed “reticulate” with polygons sharply defined; “obsoletely reticulate” with polygons indistinctly defined by shallow channels; and “smooth” with polygons absent (Seevers, 1951). These states of microsculpture grade evenly into one another, and it is difficult to assign the pattern found in many beetles to one or another of these categories.

In the most generalized condition, isodiametric polygonal microsculpture is uniform over the entire body. Loss and obsolescence of microsculpture is common and has occurred numerous times independently within the gyrophaenines. Modification of microsculpture is not uniform over the body of many beetles. For example, in specimens of *Gyrophaena fuscicollis* Seevers, the surface of the pronotum is obsoletely reticulate to smooth, while the surface of the rest of the body is reticulate. Microsculpture is lost from the entire body surface of some adults producing a uniformly markedly shining integument (e.g., *Gyrophaena vitrina* Casey).

The state of reticulation on various body surfaces is useful for recognition of some species. However, degree of loss of microsculpture varies among individuals. For example, microsculpture on head surfaces of specimens of *Phanerota fasciata* varies from smooth to obsoletely reticulate.

Other types of modification of the isodiametric pattern are uncommon. In members of some robust species of *Gyrophaena* (e.g., *G. arrowi* Bernhauer) from South America and Africa, meshes of pronotal surfaces are markedly transverse.

Faint to marked V-shaped pairs of ridges terminating distally in a seta appear to be modifications of typical polygonal microsculpture. These types of structures are associated with the setae on tergum 10 in specimens of *Sternotropa* and *Brachychara* (Figures 171, 174) and on the abdomen of specimens of *Adelarthra barbari*.

Some types of carina found in gyrophaenines may be modifications of microsculpture. In some specimens of *Gyrophaena*, carinae associated with the setose area on the metepisternum (Figures 245, 246) follow the edge of the polygons. These carinae may result from thickening of the edges of polygons to produce a continuous ridge. In some *Gyrophaena* termination of the secondary neck carina near the gula seems to have arisen in a similar way.

Among gyrophaenines, I have not observed microsculpture modified to produce markedly scaly or pointed microsculpture as described in species of pericaline lebiine carabids by Ball (1975). Nor have I seen examples of meshes terminating in micropoints as described in gymnosine aleocharines by Hammond (1975).

Other types of integumental surfaces are found among gyrophaenines, and, though distinct from the isodiametric system of microsculpture discussed above, these modifications are small, present over a more or less substantial portion of the body, and affect the physical appearance of the integument. Therefore, these types of integumental modification, discussed below, are considered as microsculpture.

A common integumental modification is development of small point-like elevations usually associated with setal insertions. The surface of the integument is raised into a small point with

the seta inserted apically. Such small elevations are called "asperities". Numerous and closely arranged asperities, a condition termed "asperitely punctate", give the surface a rough, granular or dull, appearance. Asperities may occur in any area where setae occur, and are densest in areas where setae are most numerous. Insertions of both microsetae and macrosetae may be asperite. Asperities are found throughout the setose areas on a beetle, or are limited to one or more loosely delimited areas. They are commonly limited to, or more prominent on, the outer angles of the elytra.

Simple point-like asperities are modified in a number of ways, generally as an enlargement of the asperity to form a distinct mound, or, in more extreme examples, a spine with a seta at the end. Usually, this spine is elongated in the antero-posterior plane of the beetle. Under these circumstances the asperity is a short, low ridge or carina with the highest point most distal. These modified asperities are densely packed together as in the asperite apical angles of the elytra of *Gyrophaena sculptipennis* Casey, or widely separated and distinct as in the small carinae on tergum 7 of members of the *Gyrophaena nana* species group. Spines and carinae resulting from modifications of asperities are quite prominent in some adults. These more prominent modifications are commonly associated with secondary sexual characteristics, particularly in male specimens.

**Setation.**— Setal patterns on the body of gyrophaenines are arranged in two groups in which setae differ in prominence, permanence and characteristic types of modifications. The body of gyrophaenines is covered with a general vestiture of "microsetae". In the most generalized condition, this system consists of a uniform covering of short, densely arranged setae. Modifications of microsetae involve changes in the shape and size of setae or changes in the number and density on body surfaces, and general reduction of setae on one or more body parts. No particular setae or patches of setae in this group appear to be stable under modification.

Scattered among the microsetae are longer, darker, macrosetae with a relatively fixed position and orientation. Individual macrosetae have a permanence in location and expression not characteristic of microsetae. Modification of macrosetae is by enhancement, reduction, or loss.

**Microsetae:** Arrangement and orientation of microsetae, particularly on pronota and elytra, provide a number of characteristics for classification of aleocharines. These patterns have been used for classification of European aleocharines, especially athetines, since Brundin (1942, 1943 and others) and Hoeg (1945) described and emphasized the usefulness of these patterns in generic level classification. However, they have not been used for classification of the North American aleocharines previous to Seevers (1978) who described and provided illustrations of the microsetal patterns on the pronota and elytra of these beetles.

Among gyrophaenines, pronotal setae are directed caudad and more or less parallel, or are directed caudad and latero-caudad, usually radiating from a mid-apical point (Patterns A and B of Seevers, 1978). Because of lack of variability in this basic pattern, microsetal orientation and distribution have relatively little use in generic level classification of gyrophaenines.

The generalized condition among gyrophaenines appears to be a uniform body covering of short, densely arranged microsetae. Modification of the generalized condition includes changes in length and structure of setae, and/or reduction, enhancement of setae on, or loss from, one or more body regions. These modifications will be discussed more completely under discussion of the appropriate body region.



**Macrosetae:** Most macrosetae are longer, darker and more conspicuous than microsetae. However, in specimens of some gyrophaenines it is very difficult to distinguish between the two groups. In those instances in which macrosetae are difficult to recognize, it is often possible to distinguish them in slide preparations by differences in orientation from the more numerous microsetae.

Because of the greater constancy in location and expression of macrosetae (in comparison to microsetae), presence, absence, and degree of development of individual macrosetae are very useful characters at both inter- and intrageneric taxonomic levels. Variation in macrosetal characters is described under discussion of character systems in the appropriate body region.

**Head.**— A number of character systems on the heads of gyrophaenines is available for use at various taxonomic levels. Commonly, states of these character systems form a continuum and make precise determination of character states difficult or impossible. Therefore, standardization of measurements is important. Measurements used for head dimensions in this study are described above.

Generally, a gyrophaenine head is prognathous, that is, the head is in the plane of the body with mouthparts directed anteriorly. However, in some species of *Sternotropa*, *Agaricomorpha*, *Brachychara* and *Encephalus*, heads are more or less deflexed and hypognathous. Also, species of *Brachychara* and *Adelarthra* are unusual among gyrophaenines in that the base of the head is covered by the anterior margin of the pronotum.

Basic shape of the head is determined by variation in at least three independently varying dimensions. These are width:length ratio, size and position of eyes, and length and shape of temporal region. The width:length ratio is a measure of relative transversality of the head. Among gyrophaenines are species with quite transverse heads (*Adelarthra barbari*, W:L=1.7) to those with the head longer than wide (*Gyrophaena gracilis*, W:L=0.8, Figure 8). Most specimens of *Sternotropa* (Figure 17), *Agaricomorpha* (Figure 20) and *Brachychara* (Figure 19) have relatively transverse heads. In contrast, most species of *Gyrophaena* (Figures 9–11), *Phanerota* (Figure 12) and *Eumicrota* (Figure 14) have heads which are only a little wider than long. Specimens of the *strictula* group of *Gyrophaena* (Seevers, 1951) (=subgenus *Phaenogyra*) have the most quadrate heads among the gyrophaenines.

Position of eyes in gyrophaenines is generally lateral. However, in specimens of *Adelarthra barbari*, *Brachychara* species (Figure 19), and many species of *Sternotropa* and *Agaricomorpha* eyes are relatively far forward on the head and are directed more or less forward.

Eye size is difficult to estimate. Seevers (1978, p. 23) compared the length of eyes to distance of an eye from base of head. This appears to be an unsatisfactory comparison because two independent variables, eye size and length of temporal region, are being compared. In this method of comparison, absolute eye size can remain the same, and relative eye size vary by change in development of the temporal region among species. Because all proportions of the head may vary independently, the comparison which most consistently reflects relative eye size (and thus overall contribution of eyes to appearance of the head) is length of eyes in relation to total head length, and is used in this study. Comparison of eye size to total head length suffers from an error factor similar to that of comparing eye length to temporal length, that is, head length may vary independently of eye size. However, head length does not vary to the extremes that development of the tempora does among gyrophaenines. Also, the effect of eye size on head shape and habitus of an insect in general seems to be mostly an intuitive comparison of eye size to total head size. A more absolute comparison of eye size may be possible by comparing the

eye to some unrelated structure on the same beetle, such as the scape of the antenna. However, this comparison suffers from the same deficiencies unless it can be shown that the structure being compared with eye size varies only with overall size of the beetle.

In most gyrophaenine species, the eye length is about half, or slightly less than half, head length, though variability is great. The smallest eyes relative to head length are those of members of *Adelarthra barbari*, species of *Brachychara* (Figure 19), and some species of *Agaricomorpha*. The largest eyes are found in members of the genus *Phanerota*. Eyes in specimens of this genus are among the largest in relation to size of beetle known among aleocharines. Eyes of members of *Phanerota* occupy almost the entire lateral margins of the head (Figures 12, 13).

The temporal region of the head varies considerably among gyrophaenines. Specimens of most species have a relatively well developed temporal region, with the head curved broadly behind the eyes to the base of the neck. In specimens of some species (e.g., *Adelarthra barbari*, and some species of *Gyrophaena*, Figure 7), the sides of the head capsule converge from behind the eyes to the base of the head. In some species (e.g., *Gyrophaena strictula*) the head is quite quadrate with the base more or less angulate. Because of the very large size of the eyes, specimens of *Phanerota* have a very short temporal region.

The dorsal surface of the head of gyrophaenines has a number of microsetae on it. These microsetae are short, stiff, numerous and densely arranged (members of *Agaricomorpha*, Figure 20; *Eumicrota*, Figure 14; and others); numerous, long and silky (*Probrachida*; *Brachida*); long and scattered (most *Gyrophaena* species, Figures 7–11); or numerous and very fine (*Brachychara* species, Figure 19). Structure and distribution of microsetae on the head of gyrophaenines seems to have undergone modification independently a number of times. Probably, presence of numerous short, stiff, closely spaced setae is the ancestral state. Reduction in number of setae and modification to produce longer or finer setae has occurred a number of times.

Macrosetae are absent from the heads of most gyrophaenines. However, there are a few notable exceptions. Heads of specimens of many species of *Brachida* (e.g., *B. exigua*, Figure 15) have a pair of macrosetae medially on the vertex. A very few species of *Gyrophaena* (e.g., *G. egena* Casey, Figure 10) have a pair of macrosetae in a similar location. It is not clear whether these macrosetae are homologous in specimens of those genera where they occur. Also, distribution of these macrosetae gives no clue about whether their presence is a derived or ancestral character state within the gyrophaenines.

In addition to this pair of medial macrosetae, many members of the subgenus *Acanthophaena* of *Phanerota* have two macrosetae on each side of the head medial to the eyes (Figure 13). Since no similar macrosetae are known among other gyrophaenines, these must be considered uniquely derived within *Acanthophaena*, probably by modification of microsetae.

All known gyrophaenines have an infraorbital carina (postgenal carina of Seevers, 1978). Seevers (1951) believed the large eyes of members of *Phanerota* crowded out the infraorbital carina so that members of this group lack this structure. However, he was incorrect. The large eyes of *Phanerota* species do indeed impinge on the infraorbital carinae, but they are present along the inner margin of the eye. Development of the infraorbital carinae may be quite marked (e.g., many *Probrachida* species), quite weak (e.g., specimens of the *pulchella* group of *Gyrophaena*, Figure 11), or, more commonly, moderately but distinctly developed (Figures 7, 14, 20). Ventrally, the infraorbital carina extends from near the anterior margin of the eye beneath the eye, then dorsally at varying distances behind the eye, across the dorsal surface of

the head as a continuous subbasal ridge or carina. In some species, the infraorbital carina is incomplete dorsally either as a result of gradual fading dorsally, or by the carina terminating near the baso-lateral angles of the head.

In addition to the infraorbital carina, all known gyrophaenines have a more posterior carina on each side of the ventral surface of the head. Depending on the species, this carina is (Figure 14) or is not (Figure 16) extended ventro-medially to contact the gular sutures. This carina also extends around the sides of the head, and in most species, terminates dorso-basally (Figure 11).

In some gyrophaenines (*e.g.*, *Agaricomorpha apacheana* (Seevers), Figure 20) a third carina is present at the base of the head.

Other interesting characters of uncertain value on the head include relative length to width ratio at narrowest point of gula. Changes in this character seem to be related to head length. In addition, in a few gyrophaenines, the antero-lateral angles of the gula are more or less expanded to cover the base of the cardo of the maxilla (*e.g.*, some species of *Probrachida*).

*Antenna.*— Seevers (1978) pointed out the usefulness of antennal characters for classification of genera and species of aleocharines, using antennal characters extensively as important key and diagnostic characters, particularly in revision of the difficult “athetine” complex.

Actually, the number of character systems known in the antenna of aleocharines available for use at various taxonomic levels has been increasing slowly but steadily in the literature. Variation occurs principally in relative lengths and widths, and structure and setation of antennomeres, presence, absence and/or type of specialized sensilla, and overall general form. Use of antennal characters in classification of the aleocharines is presently limited by a general lack of information about variability in character systems at different taxonomic levels. As information on this variability accumulates, antennal characters are likely to become more important. In addition, more comprehensive comparative studies are likely to reveal new and presently unsuspected character systems.

Casey (1906) first used antennal characters extensively for classification of gyrophaenines. He concluded that, among the gyrophaenine genera he recognized, the antennae were variable within the generic limits of *Gyrophaena*. At superspecific levels he recognized several important characteristics. Among most gyrophaenines, the antennomeres 1-4 are distinct from 5-11, and form a distinct pedicel for the more apical antennomeres. He also recognized that antennomere 3 is consistently longer than 4, and in most, 4 is the shortest in the antenna. In addition to these general characteristics, he noted that antennomere 4 resembles either the apical antennomeres or the basal three in sculpture, setation and structure. He used this mostly in characterization of bolitocharine genera. I have not seen this character used by other authors, but it is of value at some taxonomic levels.

Based on setation, sculpture and form, the antennae of many aleocharines, especially gyrophaenines and bolitocharines, include two distinct parts: a basal portion with antennomeres weakly sculptured, with fewer, more scattered setae, and more or less conical in form, enlarged more or less gradually from base to apex; and an apical portion with antennomeres more densely sculptured, with more and denser setation, and more or less cylindrical in form, with a distinct basal angle. Among gyrophaenines the basal portion of the antenna includes either antennomeres 1-3 (Figure 27) or 1-4 (Figure 24). Most gyrophaenines have the basal portion of the antenna made up of antennomeres 1-4; only specimens of *Probrachida* have the former condition. Despite the possibility that states of this character system vary continuously among

individuals of species or higher taxa, it is seldom difficult to assign an antenna found among gyrophaenines to one state or the other. (A few species of *Brachida* have antennae which show intermediate states which are somewhat difficult to interpret). Based on the distribution of states of this character in bolitocharines and other aleocharines, it seems likely that resemblance of the fourth to the apical antennomeres is the primitive condition. If this is correct then modification of antennomere 4 to resemble the basal antennomeres has occurred independently a number of times in bolitocharines and gyrophaenines.

A number of additional patterns of antenna structure are recognizable. Generally these patterns result from variation in the relative lengths and widths of antennomeres, particularly 5-10. These patterns affect overall appearance of an antenna. Often more than one pattern may be observed in the same antenna.

Patterns of variation of relative lengths and widths of antennomeres found among gyrophaenines include:

1. Antennomeres 5-10 transverse (Figures 21, 26).
2. Antennomeres 5-10 elongate (Figure 24)
3. Antennomeres 5-10 increase gradually in width from basal to apical antennomeres (antenna appears incrassate) (Figure 21).
4. Antennomeres 5-10 uniform in width (forming a loose, parallel-sided club) (Figure 26).
5. Antennomeres 5-10 increase in relative length from base to apex (Figure 22).
6. Antennomeres 5-10 decrease in relative length from base to apex (Figure 24).
7. Antennomere 4 elongate (Figure 23), quadrate (Figure 22), or transverse (Figure 26).
8. Antenna loosely organized (Figure 23).
9. Antenna tightly organized (Figure 21).

Among gyrophaenines, these patterns are stable at a variety of taxonomic levels. Therefore, one or more of these patterns may be useful for diagnosis, characterization or analysis at several taxonomic levels, depending on the group under consideration.

Because similar types of antennal structure have almost certainly evolved a number of times within the gyrophaenines, it is impossible to use antenna structure exclusively to delimit major groups within the gyrophaenines. Seevers (1951) recognized this and rejected the subgenus *Leptarthrophaena* Scheerpeltz and Höfler of *Gyrophaena* because it was based solely on antennal characters. He also transferred the species included in the subgenus into several species groups.

However, because patterns of antennal structure vary in the same way within some groups, antennal structure frequently correlates well with other characters, such as aedeagal type or secondary sexual characteristics. Therefore, antennal structure may be very useful at a variety of taxonomic levels if considered in combination with other character systems. Patterns of antennal structure may be especially useful in recognition of species groups within such large genera as *Gyrophaena*.

In addition to the general patterns discussed above, relative lengths and widths of various antennomeres are reliable and very useful species recognition characters in many groups of gyrophaenines. Seevers (1951) used this character system extensively even though he mainly distinguished species by aedeagal characters.

I have not found any specialized sensilla on the antennae of gyrophaenines which might be useful for taxonomic purposes.

**Labrum.**— Seevers (1978) stated that the labrum of aleocharines varies little and therefore has “little diagnostic value”, supposedly for generic level classification. However, number and position of major setae, development, structure and relative position of major sensory elements, and presence of other characteristics such as sutures and internal setal patches vary considerably both among genera and among species. The labrum, therefore, offers a number of potentially useful character systems at various taxonomic levels.

Sawada (1970, 1972) discussed the basic structure of the aleocharine labrum and proposed terms for major setae and sensory elements.

The general outline of the labrum of aleocharines is broadly oval or trapezoidal. The surface bears a number of setae and sensory elements. Among these setae, Sawada (1970, 1972) recognized three pairs of large, suberect and darkly colored setae on each side. He distinguished three transverse rows per side, each made up of two setae. He called these rows the “distal”, “medial” and “proximal” rows, and named the setae d1 and d2, m1 and m2, and p1 and p2 respectively, with the more medial seta of each row designated number 1 and the more lateral number 2 (Figure 1A).

In addition to major setae, there are a number of sensory elements (called “setulae” by Sawada) on the labrum. There is a concentration of sensory elements medially on the anterior margin. Sawada recognized three distinct pairs of sensory elements in this concentration (Figure 1A). These are: “a”, a distal setiform sensillum; “b”, conical and more medial; and “c”, more proximal and robust, with an exposed tip.

In some taxa a pair of membranous lobes is associated with this anterior concentration of sensilla. These lobes arise on either side of the b-sensilla, and are very large (specimens of *Gyrophaena* and *Phanerota*, Figures 29, 30, 34), quite small and difficult to distinguish (*Probrachida modesta* (Sharp), Figure 37), or virtually absent (*Probrachida carinata* (Sharp), Figure 38). The base of the a-sensillum arises in these lobes in many taxa.

Sawada recognized that these setae and sensory elements were present in most aleocharines, and that their character states could be useful in classification. However, to provide a more generally useful system, especially for discussion of variation among gyrophaenines, Sawada's system of terms for setae and sensory elements must be modified and extended.

Number of setae on the labrum varies considerably: numerous and dense (*Brachida densiventris* Bernhauer, Figure 43 *Probrachida sparsa* (Sharp), Figure 39), reduced to only a few pairs of well developed setae (specimens of *Gyrophaena*, Figure 29; *Phanerota*, Figure 33; *Eumicrota*, Figure 35), or with a variety of intermediate states of number of setae (*Brachychara* sp., Figure 54; *Encephalus americanus*, Figure 36).

The simplest labral setation among gyrophaenines is found in specimens of *Gyrophaena*, *Eumicrota* and *Phanerota*. On the typical labrum of members of these groups distal, medial and proximal pairs are well developed and easily recognized. There is also a single seta medially on each side of the midline. For clarity, I believe a less ambiguous set of terms should be applied to these setae. Therefore, I recognize three lateral pairs of setae on each side of the labrum: an apical lateral pair, A.L.1 and A.L.2 (d1 and d2 of Sawada); a medial lateral pair, M.L.1 and M.L.2 (m1 and m2 of Sawada); a basal lateral pair, B.L.1 and B.L.2 (p1 and p2 of Sawada); and the single seta on each side of the midline, the paramedial or PM. This set of terms is illustrated in Figure 1B.

These major setae are distinguishable on the labrum of all gyrophaenines, although the homologous setae become difficult to identify in those species with a highly setose labrum. Furthermore, these setae seem to be invariant under reduction so that although the number of setae has been reduced a number of times independently within the gyrophaenines, these particular setae have rarely been lost or significantly reduced.

In those in which the labrum is densely setose (e.g., *Probrachida sparsa*, Figure 39), A.L.1 and A.L.2 can generally be recognized by their occurrence most near the apical and lateral margin, though quite far removed from the margin in several species of *Probrachida* (Figures 37, 38, 39). Seta M.L.2 of most specimens is recognized by its greater length in comparison to other setae, but M.L.1 on some specimens is difficult to distinguish. It is usually more proximal and slightly medial to the  $\epsilon$ -sensillum (see below). This characteristic position is helpful in recognizing M.L.1 in species with an intermediate number of setae (e.g., *Brachychara*, Figure 54, or *Probrachida geniculata* (Sharp), Figure 40). However, this position is not invariable and helps little in distinguishing this seta in specimens of some species (e.g., *Brachida densiventris*, Figure 43; *Probrachida sparsa* (Sharp), Figure 39). Setae B.L.1 and B.L.2 are usually recognized by dark color and large size. In addition, these setae often diverge laterally, while other setae converge medially.

I have not been able to find a way to recognize which setae are homologous to PM in species with a densely setose labrum.

Other than those gyrophaenines in which the labrum is densely setose, the most common variations in labral setation are an additional seta on each side of the midline anterior to PM (e.g., *Brachida sublaevipennis*, Figure 45) and one or more setae between M.L.1 and M.L.2 (e.g., *Encephalus americanus*, Figure 36), or proximal to M.L.1 and M.L.2 (e.g., specimens of *Brachychara*, Figure 54).

It is important to note that among other aleocharines, these setae are not as stable under modification as they are among gyrophaenines. However, they serve as useful reference points for discussion of chaetotaxy of the labrum.

A number of sensilla (setulae of Sawada, 1970) are on the labrum of aleocharines. Three pairs of sensilla recognized by Sawada (1970), concentrated medially on the anterior edge of the labrum, are borne by all gyrophaenines. These comprise the "antero-medial sensory area". Position, shape and relative development of these sensilla vary considerably from species to species within a genus.

The terms Sawada (1970) used to refer to these sensilla are here modified to reduce possible confusion with terms for setae. The  $\alpha$ -sensillum (a-sensillum of Sawada, 1970) is most commonly seta-like (Figure 31). Rarely, it may also resemble a short, stubby spine (e.g., *Brachida sublaevipennis* Cameron, Figure 45), or be modified to a hyaline, thickened spine (*Probrachida undescr.* sp., Figure 41). Seta-like  $\alpha$ -sensilla are quite large (e.g., *Probrachida geniculata* (Sharp), Figure 40), more normal sized (e.g., *Gyrophaena frosti* Seevers, Figure 31), or quite small (e.g., *Phanerota dissimilis* (Erichson), Figure 34; *Encephalus americanus* Seevers, Figure 36). Usually the base of the  $\alpha$ -sensillum is found in the membranous lobe on each side of the midline (Figure 32), but when these lobes are poorly developed or absent, the base of the sensillum is in the main body of the labrum. Several species of *Gyrophaena* (Figure 29) have an additional small secondary sensillum at the base of the  $\alpha$ -sensillum.

Emerging medially (between the membranous lobes when these are present) is a pair of peg-like sensilla, the  $\beta$ -sensilla (b-sensilla of Sawada, 1970). Development of this pair varies

from very prominent (e.g., *Gyrophaena antennalis* Casey, Figure 32) to quite small (e.g., *Brachida sublaevipennis*, Figure 45).

The  $\gamma$ -sensillum, one on each side, (c-sensillum of Sawada, 1970) is proximal and usually lateral to the  $\beta$ -sensillum. The  $\gamma$ -sensilla are usually expressed as small internal bulbs with small conical exposed tips. Development and position relative to other elements of the antero-medial sensory area vary intergenerically and interspecifically in some taxa.

On each side of the antero-medial sensory area, on the anterior margin of the labrum, is a single seta-like sensory element, the  $\epsilon$ -sensillum. This sensillum is present in most gyrophaenines. It is near the lateral edge of the anterior membranous lobes in most of those species in which these lobes are well developed. Development of the  $\epsilon$ -sensillum among the gyrophaenines ranges from virtually indistinguishable from a seta (e.g., *Brachida sublaevipennis* Cameron, Figure 45), to virtually absent (e.g., *Pseudoligota varians* Cameron, Figure 51). In specimens of most species it is seta-like and more or less prominent. Development of this sensillum is quite uniform among individuals within a species, but varies among species within a genus. Ubiquity of the  $\epsilon$ -sensillum makes it a useful reference point for establishing chaetotaxic homologies.

Along each lateral margin of the labrum are a number of short, spine-like sensilla arranged in a semicircular row, the "lateral sensory row". In most species there are three or four sensory elements in this row (Figure 33), but there may be as many as five (e.g., *Phanerota dissimilis*, Figure 34), or only one or two slightly developed spines, or the elements are virtually absent (e.g., *Encephalus* species, Figure 36, and many *Sternotropa* and *Pseudoligota* species, Figures 48, 51, 52). The sensilla of the lateral row are near or at the lateral margin (most species of *Brachida*, Figures 43-45; *Probrachida*, Figure 37-39, and *Sternotropa*, Figure 50), or more or less distant from the lateral margin (many *Gyrophaena* species, Figure 30; many *Eumicrota* species, Figure 35; and *Phanerota*). Distance of the lateral sensory row from the lateral margin seems to be more or less uniform within a genus or even at a higher taxonomic level, although secondary modifications make this character system difficult to interpret.

In addition to the character systems discussed above, internally on the labrum of some species of *Brachida* and *Probrachida* (Figure 41) is a patch of densely arranged fine hairs on each side of the midline. This patch is absent from the labrum of all other gyrophaenines.

The labrum of some species of *Brachychara* has a longitudinal suture-like clear area medially (Figure 54).

**Mandibles.**—Mandibles of aleocharines are rather robust, markedly sclerotized structures. In most, the right mandible bears a more or less well developed internal tooth so that the mandibles are typically asymmetrical. Also, in some, the apex of one or both mandibles is bifid and/or part of the inner margin of the mandible is serrate. An internal membranous lobe, the prostheca, is well developed on the mandibles of aleocharines. The inner margin of the prostheca is finely ciliate or serrate.

Among gyrophaenines, the tooth on the inner face of the right mandible may be slightly (Figure 70), moderately (Figure 60), or markedly (Figure 56) developed. The medial area of the inner fringe of the prostheca is made up of bifid structures (Figures 57, 67). Though these structures are not limited to gyrophaenines, they are very characteristic of most members of the subtribe. However, some *Brachida* (Figure 65) have the medial area of the inner fringe of the prostheca with spine-like or setiform, rather than bifid, structures.

Specimens of *Brachida* have the left mandible bifid at apex (Figure 65) and specimens of a few species of *Probrachida* have both mandibles bifid at apex.

The molar region of gyrophaenines is characterized by rows of small denticles or teeth. These denticles are very numerous (e.g. some *Probrachida*, Figures 63, 64) moderately numerous (e.g. most *Gyrophaena*, Figure 56), or very few (some *Pseudoligota*, Figure 70). These denticles are also on mandibles of other members of the tribe Bolitocharini. Seevers (1978) suggested that these denticles may be related to fungus feeding (see below, Natural History).

**Maxilla.**— Maxillae of aleocharines provide a rich source of character systems for taxonomic and phylogenetic study. Structure of the galea and lacinia is especially valuable. Importance of maxillary structures in systematic research has been becoming more apparent for some time, and there has been an increased emphasis placed on these characters, especially by European authors. Seevers (1978) recognized the great value of character systems in the galea and lacinia, but made almost no attempt to use character systems in these structures in his reclassification of North American aleocharines. Lohse (1974), on the other hand, pointed out that classification of aleocharines should be based principally on mouthparts, but because of the difficulty of observation he provided a key based on other characters. Apparently, lack of comprehensive studies of character systems in the maxilla is the result of the use of traditional techniques.

Sawada (1970, 1972, and later papers) has attempted to provide a comparative base for study of these structures, describing the basic form of the maxilla of aleocharines. The terms proposed by Sawada suffer from several weaknesses. In general, it is a system for reference to the basic features of the maxilla only. He did not designate many maxillary structures which may provide systematically valuable character systems. Given the great variation in maxillary structure found among aleocharines, it would be premature to attempt to provide a more inclusive set of terms until a more comprehensive morphological base has been developed. Therefore, terms proposed by Sawada (1972) for maxillary structures have been used in this revision with only minor modifications and additions.

A generalized maxilla (Figure 2) is composed of five parts: cardo (c.), stipes (st.) (including palpifer), maxillary palpus (mx.p.), galea (gal.) and lacinia (lac.). The cardo is an ovate, heavily sclerotized structure which articulates with the head capsule. The cardo bears a few setae, or these are reduced or absent. The stipes is divided by distinct sutures into an inner (i.sc.), medial (m.sc.) and outer (o.sc.) sclerite. These sclerites commonly bear four setae: two distally on the outer sclerite (usually the more distal of these is the longer); and a large seta near each basal corner of the medial sclerite. The inner sclerite of many aleocharines bears a number of spiniform sensilla.

The maxillary palpus of most aleocharines is composed of four articles. Palpomere 1 is small; palpomere 2 elongate and more or less dilated distally; palpomere 3 elongate and dilated near the middle; and palpomere 4 attenuate and subulate. Members of the tribe Aleocharini and related groups have a secondary annulation of palpomere 4, so that the maxillary palpus appears to be five-articled. Palpomere 4 bears a number of sensory elements, including a well developed spiniform apical process (a.pr.). In addition, all aleocharines have a bundle of filamentous sensilla (f.s.) basally on palpomere 4. Structure of this group of sensilla differs among species.

The outer lobe of the maxilla is the galea. Sawada recognizes two parts: an elongate proximal sclerite (p.sc.), bearing sensory pores; and a membranous distal lobe (d.l.) with some basal sensilla (b.s.) and numerous setae in most species. Shape of the distal lobe of the galea and distribution and form of setae provide important character systems for use at higher



taxonomic levels within the aleocharines.

The lacinia, the inner lobe of the maxilla, varies considerably among aleocharines. Commonly, the apex of the lacinia bears a loose comb of spines with additional spines and numerous setae distributed on the inner face (see Sawada, 1972, for a discussion of variation in this structure).

Because of great variability of maxillary structure among aleocharines, the maxilla of gyrophaenines are compared, for purposes of this discussion, to the type found among members of the subtribe Bolitocharina. This comparison is useful for several reasons. First, the Bolitocharina are probably the sister group to the gyrophaenines (see below, Phylogenetic Analysis). In addition, bolitocharines have relatively generalized maxillae which are probably more similar to those of the common ancestor of gyrophaenines and bolitocharines than maxillae of any other aleocharine group.

Maxillae of various bolitocharines are shown in Figures 96, 97 and 238. In most species of bolitocharines the four stipital setae described above are present. In specimens of a few species an additional seta is present distally on the medial sclerite of the stipes. The spinose sensilla on the inner sclerite of the stipes are well developed in most species. The maxillary palpus is generalized with numerous sensilla near the tip of palpomere 4. The two or more basal sensilla of the distal lobe of the galea are setiform, and vestiture of the distal lobe is represented by numerous, closely spaced rows of unmodified setae in most species. (But note modification of galeal setae in *Bolitochara lunulata* Paykull (Figure 239).

Laciniae of most bolitocharines have a distinct comb of teeth apically (Figure 238). Teeth of this comb grade more proximally into an area of densely spaced teeth, spines and setae, proximal to which number and density of spines and teeth decrease. The entire inner face of the lacinia is densely setose in specimens of most species. Near the base of the lacinia are two or more spines separated from the spines and setae of the distal two-thirds by a more or less glabrous area.

Members of the subtribe Gyrophaenina differ from bolitocharines and are unique among other known aleocharines in that the apex of the lacinia is obliquely truncate and beset with a well differentiated patch of numerous, more or less closely spaced teeth (Figure 74). This structure, referred to as a "spore brush", appears to be adapted for scraping maturing spores, basidia and hyphae from the hymenium layer of fresh mushrooms. There is also a tendency toward reduction of teeth, spines and setae on the inner face of the lacinia. This is probably associated with reduction of function of food manipulation by the maxillae.

Co-adapted with the lacinia in relation to spore feeding are rows of setae on the outer lobe of the maxilla. The tendency among gyrophaenines has been to reduce the number of rows of setae and modify the setae to subspatulate or plate-like structures (Figure 235). In normal operation of the maxilla, these modified setae of the galea appear to provide a cup-like cap over the apex of the lacinial comb which probably helps retain food scraped from the mushroom surface.

The most generalized maxillae among gyrophaenines are those of specimens of *Probrachida* (Figures 81–84). Members of this genus have a well differentiated spore brush, but retain a few scattered teeth on the inner face of the lacinia. In addition, in some species, the setae on the inner face of the lacinia are numerous and not arranged in a distinct row (Figures 83, 84). Maxillae of members of this group are also generalized in that the setae on the distal lobe of the galea are unmodified and in numerous (6-10) rows. Members of *Probrachida* are unique among known gyrophaenines in the presence of teeth on the inner face of the lacinia. They share the presence of numerous rows of unmodified setae on the distal lobe of the galea with

some species of *Brachida* (Figures 85–87). Numerous scattered setae on the inner face of the lacinia are also found in some members of *Brachychara* (Figure 94), and *Agaricochara* (Figure 88). Other gyrophaenines lack teeth on the inner face of the lacinia, and have lacinial setae in a single well-differentiated row, and four distinct rows of subspatulate or plate-like setae on the outer lobe of the galea (Figures 235, 236).

In addition to these very useful character systems, a number of other characters in the maxilla vary among gyrophaenines. Most gyrophaenines lack setae on the cardo, but members of some species of *Gyrophaena* have a single moderate to small seta on the cardo. Many gyrophaenines have a single large seta distally on the outer sclerite of the stipes, but members of *Brachychara* (Figure 94), *Agaricochara* (Figure 88), *Agaricomorpha* (Figure 95), *Sternotropa* (Figure 89) and *Pseudoligota* (Figure 92) also have a smaller more proximal seta. The one (Figure 73) or two (Figure 95) basal sensilla of the distal lobe of the galea are setiform in all gyrophaenines. In members of some species (e.g., *Probrachida*, Figure 83) these basal sensilla are difficult to distinguish from setae of the distal lobe.

Proximal to the spore brush of the lacinia of most gyrophaenines is a row of either three or four large, contiguous, inflated, clear, colorless sensilla (Figure 74). Although quite close to the proximal teeth of the spore brush or surrounded by setae, these sensilla are easily distinguished from both by their inflated, clear and colorless structure. They appear to be either modified setae or spines. Their function is unknown. Specimens of *Brachychara* and *Probrachida* appear to lack these structures.

In addition to these sensilla, there are either two (Figure 74) or three (Figure 78) more isolated, inflated, clear, colorless sensilla on the inner face of the lacinia of most gyrophaenines. Spines in specimens of some species (e.g., *Brachida*, Figure 86) in a position similar to that in which these sensilla are usually found strengthens the hypothesis that such sensilla on the lacinia are derived from modified spines.

The row of setae on the inner face of the lacinia is very long, with a large number of setae (Figures 73, 75), or shorter, with fewer setae (Figure 92). Specimens of most species of gyrophaenines have a single spine internally at the base of the lacinial face.

Number, size and density of the teeth in the spore brush at the apex of the lacinia also vary. These teeth are relatively long and widely spaced (Figures 73, 234), or far more numerous, shorter and more closely arranged (Figures 88, 236). The extreme of the latter condition seems to be reached in specimens of *Brachychara*. In members of this genus the area covered by the spore brush is very extensive, and the spore brush is made up of many hundreds of very short, very closely spaced teeth (Figures 94, 237). This variation is of particular interest because states of this character seem to correlate, in a general way, with the broad host preferences found among gyrophaenines (see below, Evolutionary Trends). Species with members having a spore brush of numerous, short, closely spaced teeth are included in *Pseudoligota* (Figure 92), *Sternotropa* (Figures 89–91), *Agaricomorpha* (Figure 95), *Agaricochara* (Figure 88), *Brachychara* (Figure 94), and *Eumicrota* (Figure 77). Some species of *Gyrophaena* (Figure 73), *Phanerota* (Figure 75), *Encephalus* (Figure 78), *Brachida* (Figure 85) and *Probrachida* (Figure 81) have specimens with a spore brush of large, fewer, more widely spaced teeth.

Variation also occurs in several character systems in the maxillary palpi of gyrophaenines. However, this variation seems most useful at intrageneric levels rather than intergenerically. Relative length, width and structure of the maxillary palpomeres, number and distribution of setae, and development and distribution of sensilla on palpomere 4 vary among species.

*Labium*.— The generalized structure of an aleocharine labium has been discussed by Sawada (1972) and Seevers (1978). Terms proposed by Sawada for labial structures are accepted in this study (Figure 3) except that the “discal seta (d.s.)” of Sawada is here called the “medial seta (m.s.)”.

Labia of members of the Aleocharinae are composed of four parts: mentum (m.t.), prementum (p.m.), a pair of glossae (gl.) and a pair of labial palpi (l.p.).

The mentum is a more or less trapezoidal sclerite which, in most aleocharines, has three setae near each antero-lateral angle, a pair of medial setae near the anterior margin, and one or more pairs of setae on the disc or near the postero-lateral angles (Figure 3). Characters useful at various taxonomic levels among aleocharines are degree of emargination of anterior margin, relative position and size of three major setae near antero-lateral margin, presence and position of additional setae, and overall shape and proportions of mentum.

The prementum includes a median (m.a.) and a pair of lateral areas (l.a.). In most, the prementum includes a pair of medial setae (m.s.), basal (b.p.), setal (s.p.), real (r.p.) and pseudopores (p.s.) (Sawada, 1972). Presence of two medial setae is surprisingly constant among aleocharines. Gyrophaenines are unusual in that all except members of *Probrachida* (Figure 105) have a single medial seta (Figure 98) or this seta is reduced or absent (in some *Phanerota*, Figure 101).

Glossae of aleocharines are separate and relatively generalized only in the genus *Gymnusa* Gravenhorst. In other aleocharines the glossae are fused to form a “ligula” (Seevers 1978). Degree of bifurcation of the ligula has been used commonly for classification of aleocharines. Seevers (1978) believed that structure of the ligula is not as useful for classification as previously supposed, and Sawada (1972) wrote that precise degree of bifurcation of the ligula is not constant within a species. However, among gyrophaenines, I have found that general form of the ligula, whether the ligula is bifid or not, and the range of degree of bifurcation is constant within a genus or at supergeneric levels. Among gyrophaenines, at least six states of structure of the ligula can be recognized: 1) ligula entire, broadly rounded (members of *Encephalus*, Figure 103); 2) ligula short, entire, protruded, and broadly rounded at apex (members of *Gyrophaena*, Figure 98; *Phanerota* Figure 100; *Eumicrota*, Figure 102); 3) ligula short, protruded, parallel-sided, divided 1/2 to 2/3 distance to base into two more or less sharply pointed lobes (members of *Agaricochara*, Figure 110); 4) ligula short, protruded, parallel-sided, divided 3/4 to entire distance to base into two pointed or acutely rounded lobes (members of *Sternotropa*, Figure 111; *Pseudoligota*, Figure 113; *Agaricomorpha*, Figure 117; and *Brachychara*, Figure 116); 5) ligula short, protruded, divided to base into two robust, apically rounded lobes (members of *Adelarthra*, Figure 114); and 6) ligula elongate, parallel-sided, divided in anterior 1/3 into two divergent lobes (members of *Neobrachida*, Figure 115).

Distribution and development of sensory elements on the ligula are probably useful at a number of taxonomic levels within Aleocharinae. However, before these characters become available, extensive comparative studies will be required to determine distribution and type of sensory elements present and establish homologies between sensory elements in different groups.

The labial palpi of aleocharines are typically three-articled. However, fusion of palpomeres, secondary annulation, or other modifications have occurred a number of times within the subfamily. In members of the tribes Aleocharini and Hoplandrini, secondary annulation of labial palpomere 3 has resulted in an additional pseudosegment. Members of the subtribe

Silusina, tribe Myllaenini, and others, have the labial palpi modified to long filiform processes, and members of the Gyrophaenina (and a few others) have labial palpomeres 1 and 2 fused to produce two-articled palpi. Degree of development and distribution of setae and sensory elements on the labial palpus provide characters useful at a number of taxonomic levels within the Aleocharinae. Sawada (1972) has provided a discussion of distribution and terms for the setae and sensory elements on the labial palpi.

*Pronotum*.— Among gyrophaenines pronota vary considerably in general shape, length and width, convexity and micro- and macrosetation. Types of variation in these character systems are stable at various of taxonomic levels. Therefore, the pronotum provides a number of useful character systems, not only for characterization of taxa, but also for use in phylogenetic analysis.

Contributing to general aspects of "shape" of the pronotum are such characteristics as width:length ratio, general shape and degree of convexity or flattening. Members of the genera *Sternotropa*, *Eumicrota* and *Agaricomorpha* have the most transverse pronota. Most members of these genera have pronota twice as wide as long or wider. In contrast, specimens of *Gyrophaena* (*Phaenogyra*) *gracilis* Seevers have quadrate pronota not more than 1.1 times as wide as long. Among members of *Gyrophaena* this character varies from very quadrate as in *G. gracilis* described above to quite transverse as in specimens of *G. hubbardi* Seevers (1.9-2.0 times as wide as long). Specimens of most species of this large genus have pronotal length:width ratios that cluster near the midpoint between these two values.

Except among members of *Gyrophaena*, pronotal length:width ratios among species within a genus do not vary greatly. Therefore, range of this ratio among species within a genus is a useful diagnostic character. In addition, length:width ratios are very useful for species discrimination, especially in a large genus such as *Gyrophaena*, with its great variability in this character system.

The distinctive outline of the pronotum of a gyrophaenine in dorsal aspect contributes much to the general habitus of the animal. Members of the genera *Sternotropa*, *Agaricomorpha*, *Eumicrota*, *Brachychara* and some *Gyrophaena* have basally bisinuate pronota (Figures 125, 127, 130). This character state is often associated with relatively broad pronota, and contrasts with lack of basal sinuation in many members of *Gyrophaena*, *Phanerota*, *Brachida* and some others (Figures 120, 121, 123). In members of most gyrophaenine genera, presence or absence of basal sinuation is relatively constant among species. However, within *Gyrophaena* a transformation series of this character extends from bisinuate basally to lack of basal sinuations.

Another basic pronotal shape among gyrophaenines is broadly oval (Figure 123). Species with members with broadly oval pronota are included in *Gyrophaena*, *Phanerota*, *Brachida*, *Probrachida* and *Encephalus*. In specimens of many species of *Gyrophaena* (e.g., *G. nana* Paykull, Figure 119), *Probrachida* and *Encephalus* the broadly oval outline of the pronotum is interrupted by a shallow to prominent emargination medially in the posterior margin.

The pronotum is convex or more or less flattened. Degree of convexity varies considerably among gyrophaenines. Members of species of most genera have pronota which are moderately to markedly convex. Markedly convex pronota characterize, for example, members of *Brachychara* (Figure 129), *Adelarthra* (Figure 231) and some species of *Probrachida*. Members of *Brachida*, *Sternotropa*, and others have moderately convex pronota. In contrast, members of many species of *Gyrophaena* (Figure 120) and *Phanerota* (Figure 123) have very slightly convex to almost flat pronota.

Degree of convexity of the pronotum is related to another characteristic of the prothorax. The hypomera of the prothorax are either inflexed and hidden by the lateral margins of the pronotum in lateral aspect, or are deflexed and more or less visible below the lateral margins of the pronotum. Amount of the hypomera visible varies considerably among gyrophaenines from only a small portion of the anterior margin to most of the hypomera. Variation in this character also occurs among other aleocharines. Seevers (1978) suggested that the generalized form of the aleocharine prothorax may have been convex with hypomera invisible in lateral aspect. Therefore, subsequent flattening of the prothorax, exposing the hypomera would be a derived condition. This implies that exposure of the hypomera is directly related to convexity of the prothorax. While correlation between convexity and exposure of the hypomera is striking among gyrophaenines, other factors may also be involved in exposing the hypomera. A correlation between exposure of the hypomera and relative width of the pronotum is also evident. Relative narrowing of the pronotum may result in rotation of the hypomera from a markedly inflexed to a more deflexed orientation, resulting in exposure in lateral aspect. It is impossible at this time to be certain which of the factors — degree of convexity or relative width — is more important in hypomeral exposure. Probably these two factors do not vary independently and flattening of the dorsal surface of the pronotum is normally associated with a decrease in relative width.

Among gyrophaenines, the hypomeron is broadly exposed only in members of most species of *Gyrophaena* and *Phanerota*. However, variability in this character among members of *Gyrophaena* is marked, and the range extends from hypomera not visible in lateral aspect, to fully exposed. Therefore, exposure of the hypomera is not a distinguishing characteristic of *Gyrophaena* as was suggested by Seevers (1951, 1978).

Another characteristic which contributes to overall shape of the prothorax is degree of ventral deflexion of antero-lateral margins of the pronotum. Marked deflexion of this region is evident among members of *Encephalus* and *Probrachida modesta* (Sharp). Expression of this character differs considerably among gyrophaenines from the extreme examples of antero-lateral deflexion mentioned above, to lack of deflexion in most *Gyrophaena* and others.

Both macrosetae and microsetae are present on the pronotum. There is no clear correlation of variability in these two systems. Although most gyrophaenines with large numbers of well developed microsetae on the pronotum have weakly developed macrosetae, and *vice versa*, this relationship is not invariable.

Pronota of most gyrophaenines are uniformly covered by a dense vestiture of microsetae. Generally, microsetae are directed posteriorly or postero-laterally. Pronotal setal patterns among gyrophaenines correspond to Patterns A and B of Seevers (1978), and are not very useful for discrimination of taxa. Pronotal microsetae are either very short and stiff (e.g., members of *Sternotropa*, *Agaricomorpha*), long and silky (*Brachida* species), or a variety of intermediate lengths and stiffnesses. Modification of pronotal microsetae has generally been by reduction of number and prominence of setae. This reduction appears to have occurred independently in a number of lineages. Specimens of *Adelarthra barbari* Cameron (Figure 231), *Encephalus*, *Phanerota* and many species of *Gyrophaena* have pronota virtually bare of microsetae. Variation in pronotal microsetation among species within some genera (e.g., *Gyrophaena*, *Eumicrota*) encompasses a broad range of pronotal vestitures, from a dense covering of numerous stiff setae, to few, scattered, small setae. Generally, however, development of microsetae on the pronotum shows relatively less variation than these extremes among species within a genus.

Macrosetae are in three distinct longitudinal rows on each side plus an additional anterior seta on each side of the medial row (Figure 4). For ease in discussion, setae in each row are numbered consecutively beginning with the most anterior seta. The most lateral of these rows of setae begins with the seta in the antero-lateral corner of the pronotum. There are four setae in the lateral row, labeled L1-L4. Immediately mediad of the laterals is the "mesolateral" row, with three setae (ML1-ML3). Immediately mediad of ML1 on the anterior margin is a single "paramedial" seta (PM). On each side of the midline is a row of four setae, the "medials" (M1-M4).

The generalized arrangement of setae described above is found in most species of *Gyrophana*, *Phanerota* and *Eumicrota*. However, in many species of *Gyrophana*, M2 is absent (e.g., members of the "keeni group" of Seevers, 1951), and macrosetae are difficult to see in specimens of *Eumicrota*. On specimens of many species macrosetae are difficult to distinguish from microsetae, and on some can be seen only in cleared preparations by examination with a compound microscope. Difficulty of distinguishing macrosetae is often correlated with density of microsetae. Conversely, reduction in number of microsetae is commonly correlated with increased prominence of the macrosetae. This may be clearly seen in members of the genus *Eumicrota* by comparing figures of the pronotum of *E. socia* (Figure 125) and *E. corruscula* (Figure 124). These figures are somewhat misleading because the macrosetae on the pronotum of *E. socia* are much less prominent than they appear in the drawing.

Variation in macrosetae includes the following conditions. Macrosetae appear to be absent or are indistinguishable from microsetae in specimens of many species of *Pseudoligota*. ML2 is absent from some members of many genera (e.g., *Agaricomorpha*, *Brachychara*, *Sternotropa* and others). L2 is absent from members of *Brachida*, *Brachychara* and *Agaricochara*. In specimens of some species of *Sternotropa*, *Adelarthra* and *Brachychara*, L3 is more or less prominent in comparison to other pronotal setae (greatly so in *Adelarthra*).

Variation in these, and other, characteristics of development of pronotal microsetae may be useful at a number of taxonomic levels. However, before these character systems can be used confidently, a more complete understanding of both interspecific and intergeneric variation is needed.

*Elytra*.— Length and width of elytra in relation to the pronotum are taxonomically important characteristics since these attributes contribute considerably to overall habitus of a beetle.

Elytra of most aleocharines are rather generalized and longer than the pronotum. However, members of some tribes have elytra which are considerably shortened (Seevers, 1978). Small size of elytra is associated with aptery or brachyptery and hence flightlessness. Neither brachypterous nor apterous gyrophaenines are known. However, among gyrophaenines length of elytra relative to pronotal length ranges from much longer than the pronotum (e.g., members of *Agaricochara* species), to about equal to pronotal length (most *Gyrophana*, *Phanerota* and others) or slightly shorter than pronotal length (most *Brachychara*).

Lateral apical angles of the elytra are markedly sinuate (e.g., *Encephalus zealandicus* Cameron (Figure 134), moderately to slightly sinuate (e.g., *Eumicrota*, Figure 133), or not at all sinuate (e.g., most *Gyrophana*, Figure 131; *Phanerota*, Figure 132).

Both microsetae and macrosetae are on the elytra of aleocharines. Distribution and development of these setal patterns, while difficult to quantify, may be important at a variety of taxonomic levels. Among aleocharines, there are fewer microsetal patterns on the elytra than

on the pronotum. Seevers (1978) recognizes only three. Among gyrophaenines elytral microsetae are subparallel and directed caudally (Pattern R of Seevers, 1978). Microsetae are very numerous and densely distributed so that the elytra appear more or less markedly pubescent (e.g., specimens of *Brachida* species), or are very few and very sparsely distributed (e.g., specimens of *Adelarthra barbari*). Specimens of most species of gyrophaenines have an intermediate condition (e.g., most *Gyrophaena* species). Length of microsetae also differs from long and silky (members of *Brachida*) to very short and stiff (e.g., most *Sternotropa*).

In some aleocharines distribution of microsetae on the elytra is not uniform. This condition is not common among gyrophaenines, though the elytra of specimens of some species are narrowly asetose along the suture.

Figure 132 illustrates the distribution of macrosetae on the elytra of most gyrophaenines. Development of these macrosetae is quite variable among genera and species. Macrosetae are small, inconspicuous, or obsolete (most *Pseudoligota* species), moderate sized and more or less conspicuous (most *Gyrophaena* and *Phanerota*), or extremely large and very conspicuous (members of *Adelarthra barbari*). Development of macrosetae may vary among species within a genus (e.g., species of *Sternotropa*) in which instance it becomes a useful character at the species or species group level, or development of macrosetae may be relatively constant within a genus.

Setal punctures may be asperate or not. In particular, many males have large asperities on various parts of the elytra as part of the secondary sexual complex.

Elytra of specimens of some species of gyrophaenines are adorned with spines, carinae, low elevations or depressions. Most often these modifications of the elytra are, along with asperities, part of the secondary sexual complex of characters.

*Prosternum*.— Character systems of the prosternum have been used consistently by few authors. Generally, in aleocharines, the prosternum is a more or less transverse bar between and in front of the anterior coxae. In some aleocharines (members of the tribes Falagriini and Dorylomini), the prosternum is prolonged behind the anterior coxae and contiguous with or fused to enlarged mesospiracular peritremes. The posterior prolongation of the prosternum of some aleocharines is near or adjacent to lateral extensions of the prothoracic hypomera, such that the anterior coxal cavities are more or less closed behind (Seevers, 1978).

Among gyrophaenines, the prosternum is markedly (Figure 147), moderately (Figure 145), or slightly transverse (Figure 144). In general, degree to which the prosternum is transverse correlates well with the width:length ratio of the pronotum. Thus, gyrophaenines which have a markedly transverse pronotum also have a relatively transverse prosternum. However, other factors also affect expression of this character. The prosternum of some gyrophaenines is a narrow bar with little posterior extension between the coxae, but in others extends posteriorly to various degrees between the anterior coxae as a broad process. A broad prosternal process may reduce the width:length ratio of the prosternum independently of pronotal width.

The prosternum is generally horizontal, but in specimens of a few species (e.g., *Encephalus americanus*), the prosternum is more or less declivous posteriorly.

The prosternum of some gyrophaenines is ornamented by various carinae, spines, or knobs. Most specimens of *Gyrophaena*, *Eumicrota* and *Encephalus* have a fine transverse carina extended from the antero-lateral margins of the prosternum posteriorly and medially (Figure 142). A similar, but more marked, transverse carina on specimens of *Adelarthra barbari* protrudes medially as a prominent transverse tooth. Specimens of *Agaricomorpha*, *Sternotropa*, *Brachida* and *Pseudoligota* lack this transverse carina, but have a more or less

marked medial knob, carina or spine. The prosternum lacks ornamentation in specimens of some species (e.g., some *Phanerota*, Figure 144). These prosternal character states are useful at a variety of taxonomic levels. The general form of the modification (e.g., with transverse carina or with medial protuberance) is consistent among members of many higher taxa, while the specific form of the general type of modification may vary interspecifically.

In the great majority of gyrophaenines, the inner edge of the hypomera and the posterolateral margins of the prosternum are very widely separated. However, in at least one species, *Sternotropa brevicornis* Cameron, anterior coxal cavities are nearly closed behind by the approximation of these parts.

*Mesosternum and Metasternum.*— The mesosternum and metasternum provide several character systems useful at a variety of taxonomic levels. Among most aleocharines, the middle coxae are contained in deep acetabula formed by these sclerites. In specimens of most species the edges of the midcoxal acetabula are margined with a fine bead (Seevers, 1978).

Among gyrophaenines, the mesosternum is well developed and quite broad in front of the midcoxae. In specimens of many species of gyrophaenines, the mesosternum has a medial longitudinal carina. This carina is well developed and extends from the distal edge of the mesosternum to the apex of the process (e.g., specimens of *Agaricomorpha*, Figure 155), or it is more or less reduced, present only anteriorly on the mesosternum and absent or obsolete before the apex of the metasternal process. Specimens of some species lack the mesosternal carina, but have in the same position a more or less diffuse, low to very low ridge (e.g., *Brachychara*, Figure 250). Still other gyrophaenines lack any medial modification so that the mesosternum is smooth medially (species of *Gyrophaena*, *Phanerota* and *Eumicrota*; Figures 150, 151). In most instances, presence or absence of a medial carina or low ridge is constant among members of a species within a genus, or even at supergeneric levels.

Many other aleocharines have a similar carina, and a complete, well developed carina is characteristic of most bolitocharines. Probably presence of a medial longitudinal carina on the mesosternum is primitive within the gyrophaenines, and reduced conditions derived.

The mesosternum of most gyrophaenines is more or less horizontal, but the mesosternum of members of *Encephalus* is abruptly turned dorsally in front of the middle coxae so that it is more or less vertical in lateral view.

The mesosternum of most aleocharines has a medial posterior process more or less extended between the middle coxae. Among gyrophaenines, this process is very broad and extends a considerable distance between the midcoxae (discussed further below).

The beaded margin which delimits the midcoxal acetabula also delimits a pair of processes, on each of the mesosternum and metasternum, which extend more or less between the midcoxae. Among aleocharines these intercoxal processes differ in length, width, distance each process extends between the coxae, and degree of separation of apices of the processes. In those instances in which the mesosternal and metasternal processes are not contiguous, they are joined by an anterior extension of the metasternum termed the "isthmus" (Seevers, 1978). The isthmus is extended anteriorly beyond the margined apex of the metasternal process and, in most aleocharines, is in a more dorsal plane than the metasternal process. Relative development of the mesosternal process, isthmus and metasternal process between the middle coxae, and degree of separation of the middle coxae by these processes provide very useful character systems at generic and suprageneric levels. Measurement of relative lengths of these processes is discussed above (see Methods).



In members of the subtribe Gyrophaenina, the intercoxal processes are very broad between the middle coxae, so that the coxal cavities are widely separated (Figure 149). In addition, in most gyrophaenines, the mesosternal and metasternal processes are broadly contiguous or fused between the coxae, and the isthmus is absent. In specimens of *Agaricochara laevicollis* (Figure 152), the apices of the intercoxal processes are very slightly separated and there is a short isthmus (relative lengths 7:0.5:4).

The apices of the processes at the juncture are truncate or broadly rounded. The junction between the intercoxal processes is delimited by a distinct suture (Figure 149) (e.g., most *Gyrophaena* and *Phanerota*), or the processes are more or less indistinguishably fused (Figure 154) (e.g., most *Sternotropa*, *Brachychara*, and *Pseudoligota*). In many gyrophaenines with fused processes, the juncture between them is slightly beaded, or the processes are distinguished by differences in microsculpture. Under these conditions, relative lengths of the processes may be estimated. In other gyrophaenines, the processes are indistinguishably fused (e.g., in many *Pseudoligota*) and accurate estimates of the relative lengths of the processes cannot be made.

Relative lengths of the two processes provide useful character systems at the generic level in gyrophaenines. Among members of most genera, variation in this character system is relatively slight, but is quite extensive in a few genera (e.g., *Gyrophaena*). This character system should therefore be used with caution. In most members of *Agaricochara*, *Phanerota*, *Eumicrota*, *Sternotropa* and *Brachychara*, the mesosternal process attains the middle of the coxal cavities, or slightly posterior to the middle of the coxal cavities. Among members of *Gyrophaena* the mesosternal process is various from extended to slightly posterior to middle of the coxal cavities, to extended to the apex of the coxal cavities. In specimens of *Brachida*, the mesosternal process attains or almost attains the posterior margin of the coxal cavities. In specimens of *Encephalus*, the mesosternal process extends to the posterior margin of the midcoxal cavities so that the metasternal process is absent.

*Metepisternum and Metepimeron.*— These two elongate pleurites are immediately dorsal to the metasternum. In the generalized condition, these sclerites are covered uniformly with numerous irregularly scattered setae. Among gyrophaenines, this condition is present in specimens of *Probrachida*, *Brachychara* and some species of *Brachida* (Figures 158, 249). All bolitocharines (=group Bolitocharae of Seevers, 1978) and many other aleocharines also have numerous irregularly scattered setae on these pleurites.

Modification of this generalized condition has occurred a number of times in the aleocharines. Modification has in most instances resulted in reduction of the number of setae on the metepimeron to a few scattered setae near the posterior margin, and reduction of the setae on the metepisternum to two irregular rows, one well developed row, or loss of setae from this sclerite altogether.

Among gyrophaenines, in addition to the generalized state described above, three states of the number and development of setae on the metepisternum are recognized. In specimens of *Pseudoligota*, many *Agaricomorpha* and many *Sternotropa*, the setae on the metepisternum are in two irregular rows (Figures 159, 160, 248). In specimens of *Adelarthra* (and *Encephalus zealandicus* Cameron) only a few scattered setae are present on the posterior third of the metepimeron. In specimens of *Gyrophaena*, *Phanerota* and *Eumicrota* setae on the metepisternum are in a single more or less well developed row. In addition, in specimens of some species of *Gyrophaena* and *Phanerota* this single row of setae is bordered anteriorly and ventrally by a more or less indistinct carina (Figures 156, 246).

To my knowledge, this character system has not been studied previously among the aleocharines. Therefore, distribution of the states of this character, and taxonomic levels at which these characters are stable are inadequately known. The general usefulness of this character system within the aleocharines is thus uncertain. States of this character system in gyrophaenines are more or less stable at the generic or suprageneric level. However, a single well defined row of setae has apparently evolved several times within the gyrophaenines. This is indicated by presence of both numerous scattered setae and a single row of setae among members of the same genus (e.g., *Agaricomorpha*).

*Legs.*— As pointed out by Seevers (1978), legs of most aleocharines do not have outstanding characters for taxonomic study. Number of tarsomeres per leg differs in different groups, and this has been used in constructing classification systems that seem artificial (see Fenyès, 1918, 1921). However, while tarsal formula should not be ignored, it is not, taken alone, a reliable character system for recognition of monophyletic groups (Seevers, 1978).

All gyrophaenines and most other members of the tribe Bolitocharini have a 4-4-5 tarsal formula, but this formula is not limited to this group.

Aleocharines have an empodial seta between the tarsal claws. This seta is shorter than, as long as, or longer than the tarsal claws. Among gyrophaenines, the empodial seta is shorter than the tarsal claws.

Relative lengths of tarsomeres 1 and 2 of the hind leg is characteristic of many genus-level or suprageneric-level groups among gyrophaenines. Hind tarsomere 1 of gyrophaenines has a more or less distinctly developed ventro-lateral ctenidium of six to 15 or more setae (Figure 161). The ctenidium is probably involved in cleaning activities.

*Wings.*— All known gyrophaenine adults are fully winged. Since adults must seek and colonize ephemeral, unpredictable and more or less widely dispersed habitats, loss of wings seems unlikely. Should a flightless gyrophaenine be found, the apterous or brachypterous condition would suggest that its members have fundamental differences in natural history from other gyrophaenines.

Figures 137–140 show the variation in shape and vein patterns found among species of several genera of gyrophaenines. Figure 141 of the wing of *Venusia* sp. (subtribe Bolitocharina) is included for comparison. There is little significant difference in the wings examined. In general, specimens of smaller species have wings slightly more obtusely rounded apically, with less extensively developed veins.

*Abdomen.*— Abdominal structure of staphylinids has been described in detail by Blackwelder (1936) and that of aleocharines by Fenyès (1918-21) and Seevers (1978). Interpretation and numbering of segments presented by Seevers (1978) is accepted in this revision.

Abdomens of aleocharines are composed of 10 segments, the last two of which are modified in connection with the genitalia. Terga 1 to 8 each bear a pair of spiracles. Segment 1 is more closely united to the metathorax than to the remainder of the abdomen. Both segments 1 and 2 are usually covered by the elytra and are not visible in repose. Sterna of segments 1 and 2 are membranous and not distinguishable (except for a second sternum secondarily present in a few termitophilous aleocharines (Seevers, 1978)). Segments 3 to 6 have, in addition to a tergite and sternite, a paratergite and parasternite on each side. Segment 7 has no parasternites and segment 8 has only a tergite and sternite. The tergum of segment 8 has secondary sexual modifications in many aleocharines, especially in the male. These provide numerous characters for use at specific and higher taxonomic levels. In all aleocharines except *Gymnusa*, the tergite

of segment 9 is divided into two lateral lobes. Only the male has a ninth sternite.

Among gyrophaenines, general shape of the abdomen, punctation, setation and shape and proportion of sclerites provide taxonomically useful character systems. Additionally, one or more of terga 3 to 7 may have a more or less pronounced transverse concavity.

Also, among all gyrophaenines, the anterior margin of tergum 7 is modified for openings to abdominal glands. The distribution of this modification among other aleocharines is not known.

*Abdominal Tergum 10.*— To my knowledge, character systems on abdominal tergum 10 have not been previously used extensively in study of the aleocharines. However, tergum 10 contains a number of character systems of potential use at a number of taxonomic levels. These include: shape of the tergite, distribution of micro- and macrosetae, structure of micro- and macrosetae, and presence or absence of secondary sexual character states.

The generalized aleocharine condition of tergum 10 is a flat trapezoidal sclerite in dorsal aspect, with a more or less dense patch of microsetae occupying the middle of the dorsum of the tergum. Probably, in the most primitive condition, this patch of microsetae was large, occupying most of the dorsal surface, and was made up of numerous, densely arranged, unmodified setae. Most aleocharines also have three macrosetae (four in some) on each side of the tergum near the posterior and postero-lateral margins. Modification of these character systems is quite extensive among aleocharines. While these may be useful for higher classification of aleocharines, distribution and variation in states of these systems need study throughout the aleocharines before they can be applied effectively.

Among gyrophaenines a number of character systems of tergum 10 are useful in studies of classification and relationships of higher taxa. Specimens of *Probrachida* and *Brachida* exhibit the generalized condition described above (Figure 168). Specimens of *Gyrophaena*, *Phanerota*, *Agaricochara* and some *Pseudoligota* retain a more or less square microsetal patch (setae reduced in number in some species), but with microsetae more or less flattened and subspatulate (Figures 162, 164, 169). Loss of setae antero-medially and postero-laterally results in one or a few rows of setae arranged in a distinct "V". This distribution of microsetae is found only among members of *Eumicrota*. From the generalized condition, loss of setae postero-medially results in a patch with an inverted "V"-shape (here termed "chevron-shaped"). A chevron-shaped setal patch characterizes members of *Agaricomorpha* (Figure 175) and some *Sternotropa*. Continuation of this trend towards loss of setae postero-medially and antero-laterally produces a chevron-shaped patch made up of two (faintly 3 in some) distinct rows of setae. This last condition characterizes most *Sternotropa* (Figures 170, 171), members of *Brachychara* (Figure 174) and *Neobrachida*. Microsetae on tergum 10 are flattened and subspatulate in most gyrophaenines.

Additional modifications of character systems on tergum 10 found among gyrophaenines include: elongation of the tergum posterior to the setae in some *Gyrophaena* (e.g., *G. flavicornis* Melsheimer and *G. fuscicollis* species group); an additional macroseta on each side of the tergum (in males of the *Gyrophaena pulchella* species group); and secondary sexual modifications of tergum 10 in some *Gyrophaena* (particularly notable in members of the *G. coniciventr* species group (see Seevers, 1951)).

Additional study of structure of tergum 10 would probably reveal other useful character systems.

*Female genitalia.*— The vulva and vagina of most aleocharines are relatively simple. In some athetines, these are sclerotized and have spines, setae or hooks (Seevers, 1978). Brundin (1942) has illustrated characteristics of the vagina of athetines. The vagina of gyrophaenines

does not contain extensive sclerotized areas or hooks and spines. However, it would be surprising if internal structure of the vagina were not in some way modified in relation to the very complex and varied structure of the median lobe of the aedeagus. Peschke (1978) found this to be so in females of *Aleochara curtula* Goeze. However, this has not been investigated in gyrophaenines.

Spermathecae of gyrophaenines are sclerotized, the shape being characteristic of species or higher taxa in many groups. Form of gyrophaenine spermathecae is unique among aleocharines, as far as is known, in that it has a lateral plate-like flange on the neck (Figure 176). (Compare with spermatheca of *Bolitochara*, Figure 191.) The spermatheca is simple (for example, in members of *Gyrophaena*, Figure 176; *Eumicrota*, Figure 181; and *Agaricochara*, Figure 186), has the neck elongate proximal to the lateral flange (in members of *Phanerota*, Figures 179, 180), or has the neck elongate distal to the lateral flange (in members of *Brachida*, Figure 185).

*Male genitalia*.— Male copulatory organs of aleocharines have been described in detail by Brundin (1942), Welch (1964), Sawada (1972), Peschke (1978) and Seevers (1978). All of these descriptions are quite detailed and differ little in interpretation of aedeagal structure. However, they differ somewhat in terms proposed for these structures. In this treatment, I will accept those proposed by Seevers (1978). A brief summary of the more detailed account in Seevers (1978) is necessary for discussion of this structure. The aedeagus of male aleocharines is unique among staphylinids. It is made up of a more or less tubular median lobe and two mobile lateral lobes, or parameres. The aleocharine median lobe is not fundamentally different from that of other staphylinids, but the parameres are very distinctive. While parameres of other staphylinids are slender and made up of only a single sclerite, those of aleocharines are expansive and made up of at least three distinct interarticulating sclerites.

Structure of a generalized aleocharine median lobe is shown in Figure 5A. It is a more or less tubular structure with an enlarged bulbous basal portion, and a more slender cylindrical apical part. The ejaculatory duct enters an internal sac (in.s.) which is everted into the vulva of the female during copulation. In many aleocharines, membranes of the internal sac are armed with numerous spinules, plates, and sclerotized areas which probably aid in correct placement of the sac in the vulva. A slender, more or less sclerotized, flagellum (f.) is present in the internal sac. The flagellum is hollow and functions to introduce sperm into the female tract. It is very long in many aleocharines and is probably inserted into the female spermathecal duct during copulation. On the underside of the median lobe is an oval sclerite which is attached to the main body of the median lobe by a thin membrane. This sclerite, the compressor plate (c.p.) is moved by dorso-ventral muscles (dv.m.) which originate on the upper surface of the base of the median lobe. Contraction of the dorso-ventral muscles pulls the compressor plate into the body of the median lobe, increasing the hydrostatic pressure and causing eversion of the internal sac. The internal sac is retracted by a set of longitudinal muscles (l.m.) which originate on the proximal surface of the bulbous base.

The ejaculatory duct (ej.d.) enters the median lobe through the median foramen (m.f.). In front of the median foramen are a pair of condyles (p.c.) on which the parameres articulate. Sclerotized phragmata on the base of the median lobe serve as attachment for muscles of the parameres. A distal crest (d.cr.) in front of the paramere condyles and a proximal crest (p.cr.) behind the median foramen are present in many. Other thickenings for muscle attachment are present in some.

Distally, the median lobe terminates in a more or less slender apical process (a.p.). The apical process is highly modified in many aleocharines and is very useful in systematic study at both species and higher taxonomic levels.

In many aleocharines, there is a hinged sclerite, the ostial lamella (o.l.), which closes the apical orifice of the median lobe when the internal sac is in repose.

A generalized gyrophaenine median lobe is shown in Figure 5B. The gyrophaenine median lobe differs primarily in that there is no eversible internal sac. Instead, a more or less tubular or cylindrical flagellum is exerted and slides in and out of the basal portion of the median lobe in response to hydrostatic pressure or contraction of longitudinal muscles. It is not certain that this flagellum is homologous to that found in the internal sac of other aleocharines. The median lobe does not have a complex internal array of spines, plates, or sclerotized areas.

At the base of the flagellum of gyrophaenines is a more or less membranous, transparent, globular structure, the function of which is unknown.

A great many characters, useful at a number of taxonomic levels, are found in the median lobe of gyrophaenines. These modifications are too varied to discuss in detail here. They are considered further in the generic descriptions. In general, the apical process is very long and slender (Figure 197), blade-like (Figure 203), highly complex (Figure 193) or has many other modifications. The basal portion is variously modified, and the flagellum is tubular (Figure 192), very long and whip-like (Figure 197) or sclerotized and complex (Figure 194).

Parameres (Figure 6) are composed of three sclerites: the condylite (con.), the paramerite (par.), and the apical lobe of the paramerite (ap.l.).

The condylite is a relatively slender structure which articulates with the paramere condyles of the median lobe. The paramerite articulates with the condylite near the apex of the latter. The proximal 1/2 to 1/3 of the paramerite bears more or less markedly sclerotized phragmata internally for muscle attachment. In most, the distal portion of the paramerite is delimited from the basal portion by a less sclerotized "hinge zone" (h.z.). Distally the paramerite bears two independently mobile structures, the apical lobe of the paramerite (ap.l.) and the velar sac (v.s.). The apical lobe of the paramerite of most gyrophaenines is filiform and bears four large setae. Size and shape of the apical lobe and relative placement and development of the setae provide characters useful at a number of taxonomic levels. In some, the apical areas of the paramerite and the apical lobe have a number of sensory or glandular pores. The oblique row of pores on the apical area of the paramerite is particularly distinctive of gyrophaenines (Figure 218 and others), though not limited to this group.

A submembranous velar sac is a unique element of the paramere of aleocharines. The velum is a complex structure made up of contributions from both the condylite and the paramerite. The velar sac is probably sensory or adhesive and is distended by increasing hydrostatic pressure.

Among gyrophaenines, a number of useful character systems are found in the parameres. These include: variation in size and shape of apical lobe of paramerite; differences in size and placement of setae of apical lobe; differences in position and development of phragmata; and others. These are discussed more fully within the generic descriptions.

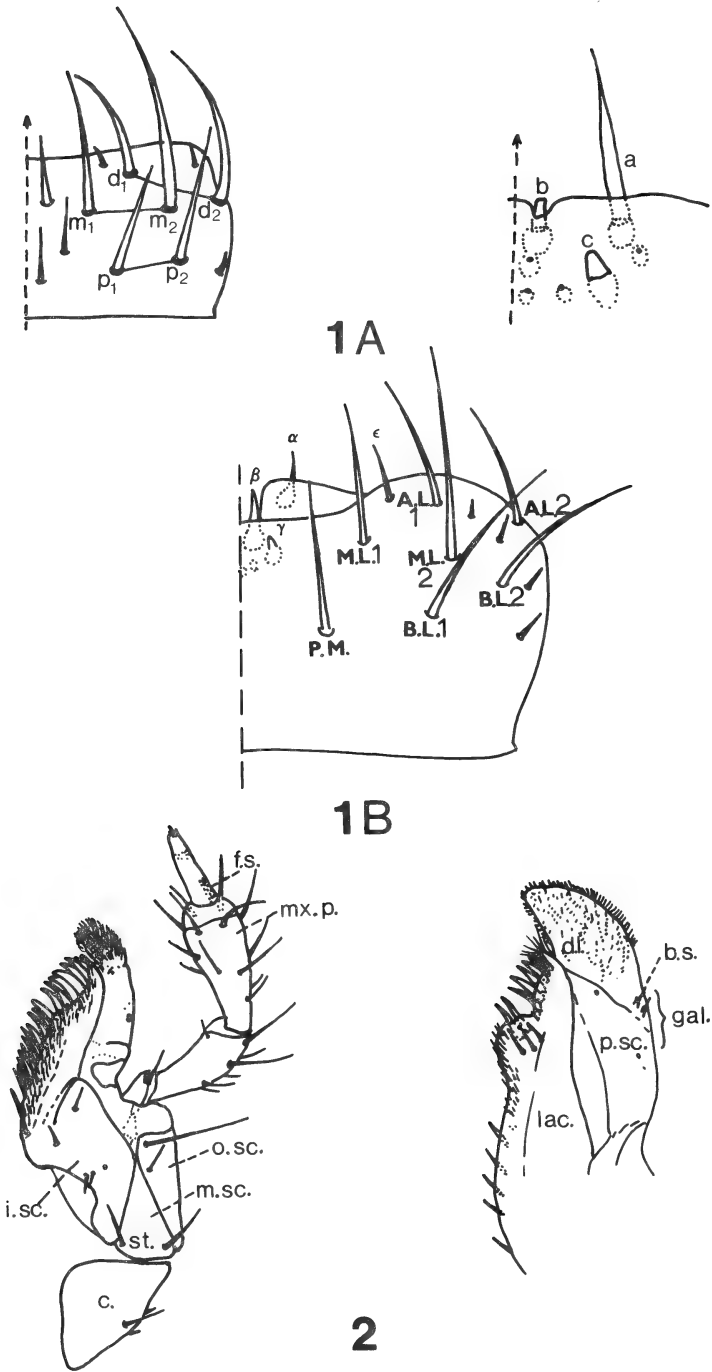
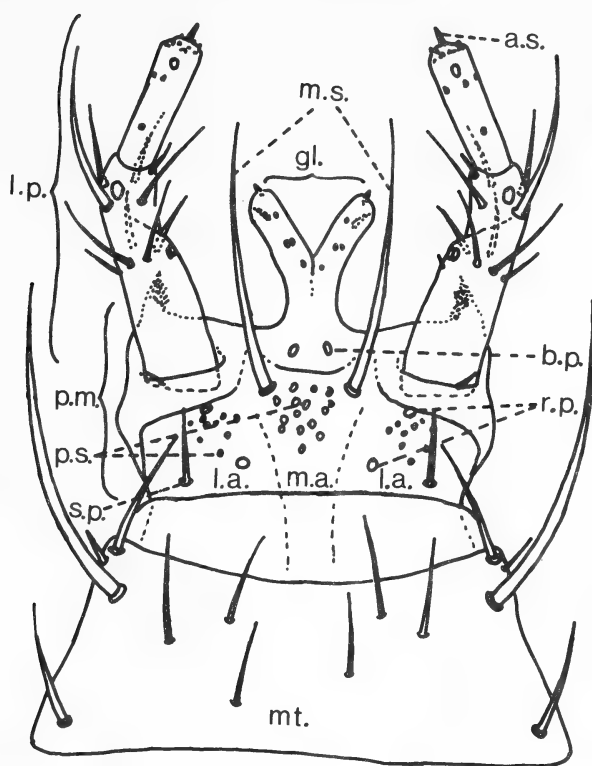
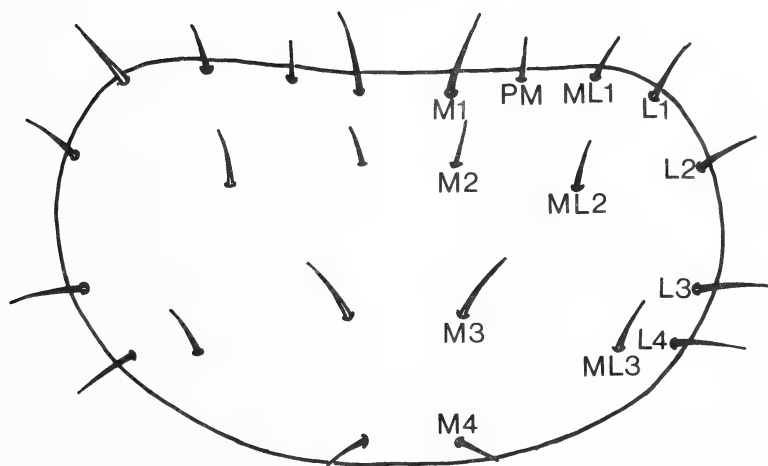


Figure 1. Terms for major setae and sensilla of labrum of adult aleocharines discussed in this study. A) Terms after Sawada (1972) (redrawn from Sawada (1972); B) Terms proposed in this study (A.L.= apical lateral; B.L.= basal lateral; M.L.= medial lateral; P.M.= paramedial). Figure 2. Terms for structures on maxilla of adult aleocharines discussed in the text (redrawn and slightly simplified from Sawada, 1971) (b.s.= basal seta; c.= cardo; d.l.= distal lobe; f.s.= filamentous sensillum; gal.= galea; i.sc.= inner sclerite; m.sc.= medial sclerite; mx.p.= maxillary palpus; o.sc.= outer sclerite; p.sc.= proximal sclerite; st.= stipes).

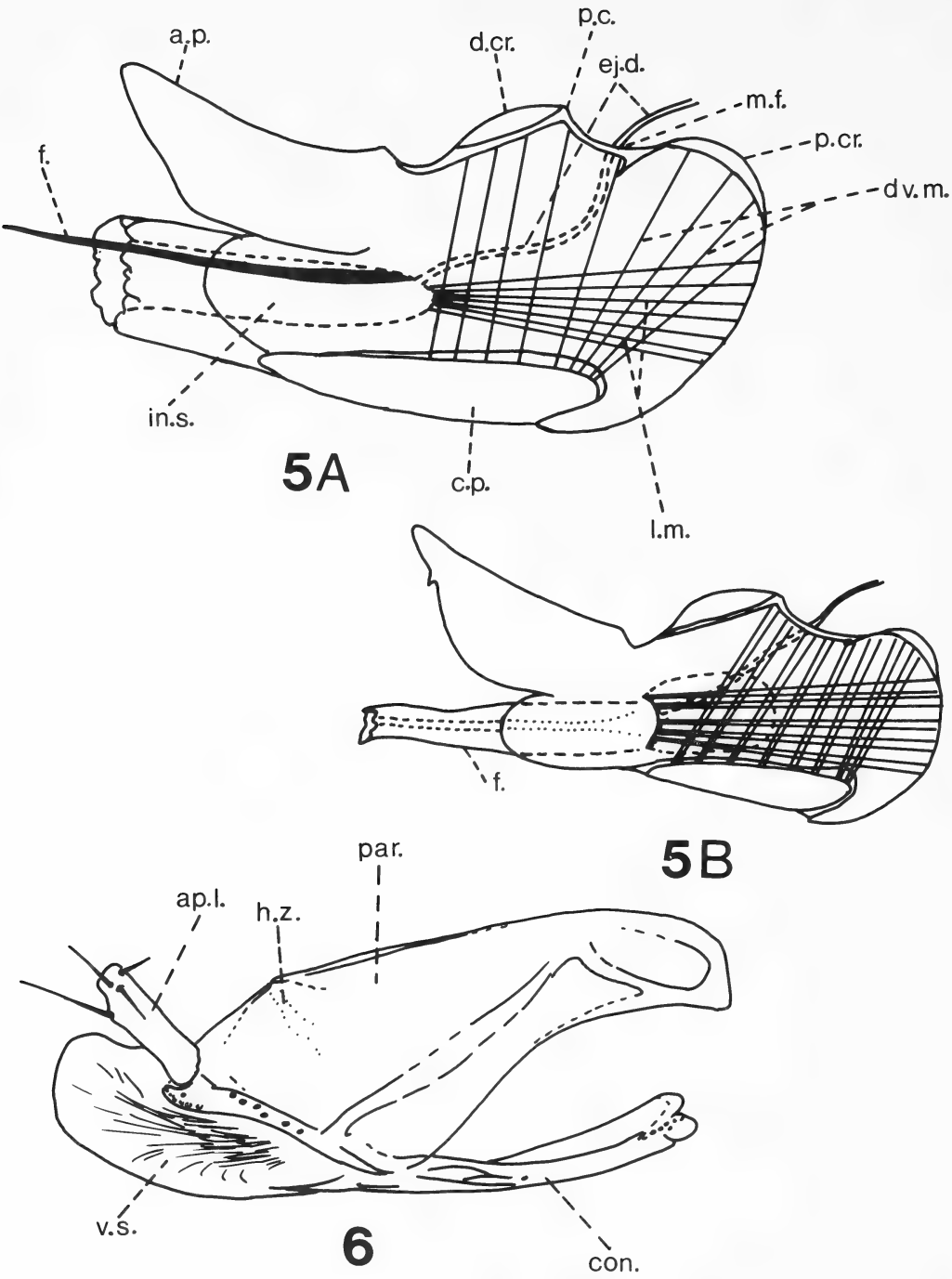


3

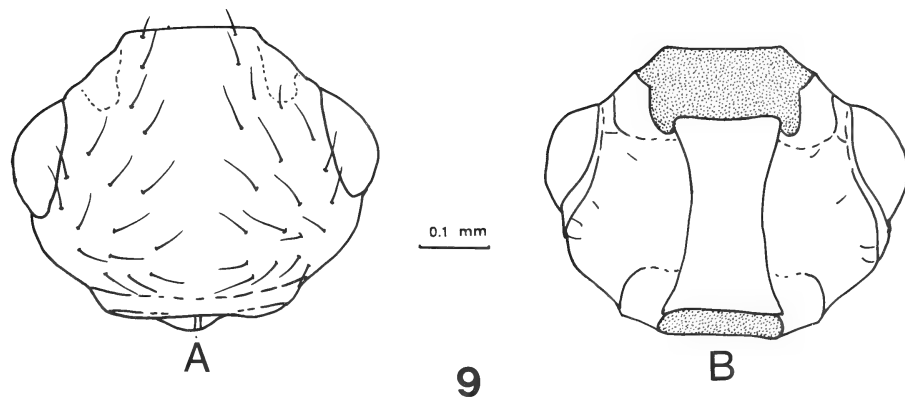
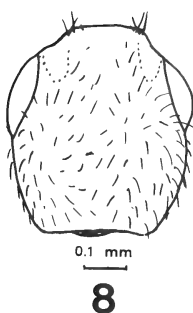
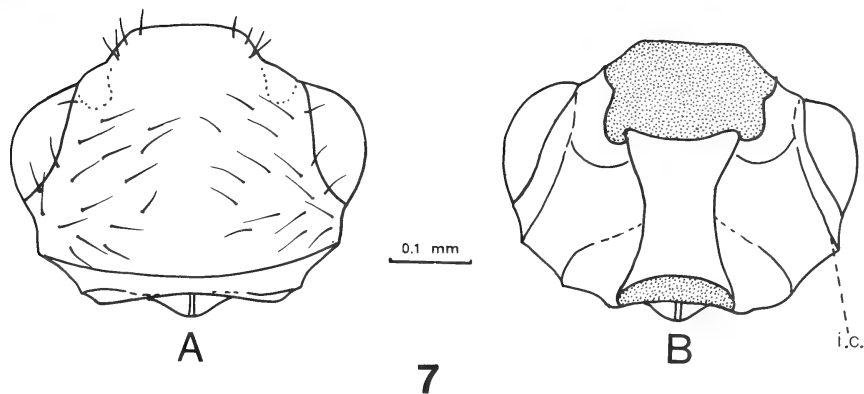


4

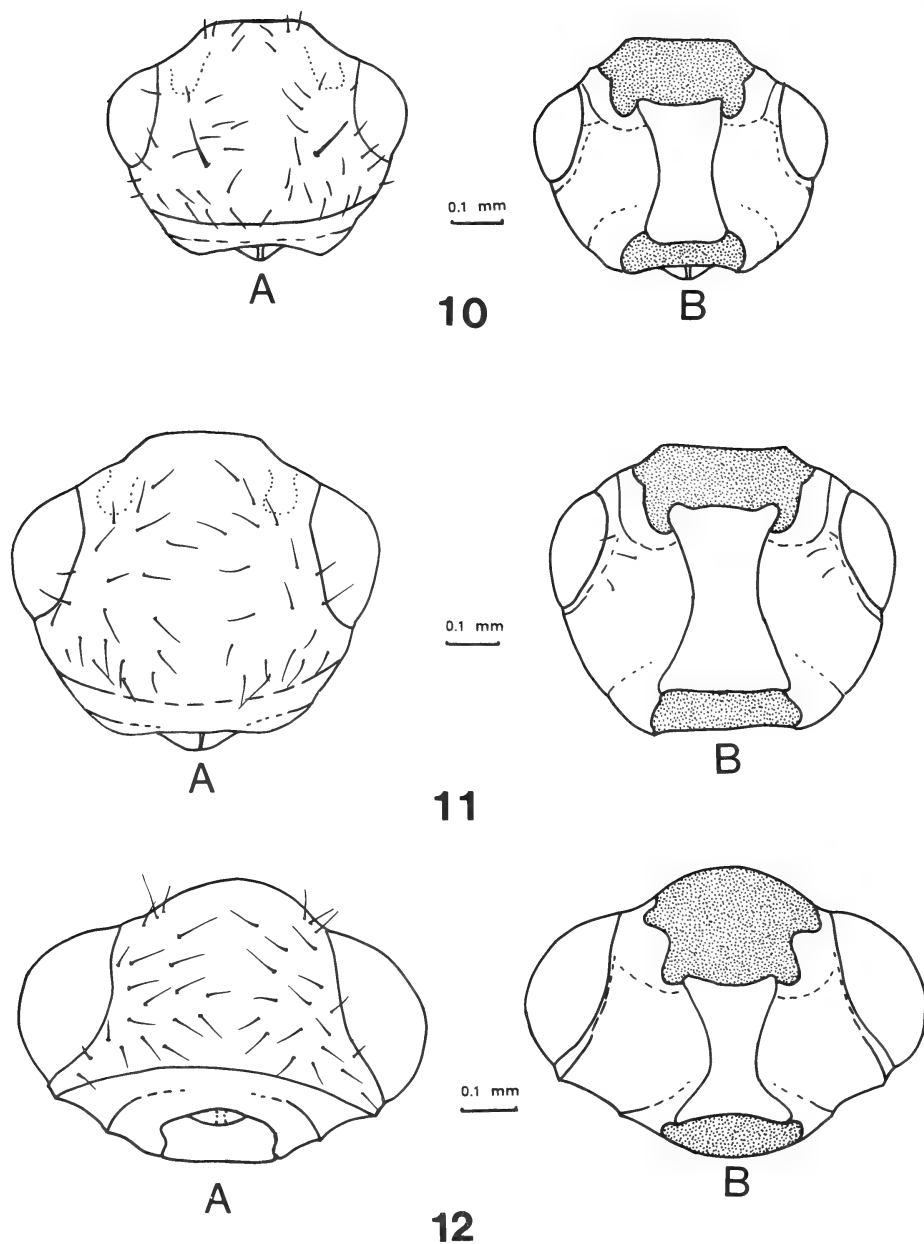
Figure 3. Terms for structures on labium of adult aleocharines discussed in the text (redrawn and slightly simplified from Sawada, 1972) (a.s. = apical spine; b.p. = basal pore; gl. = galea; l.a. = lateral area; l.p. = labial palpus; m.a. = medial area; m.s. = medial setae; mt. = mentum; p.m. = prementum; p.s. = pseudopores; r.p. = real pores; s.p. = setal pores). Figure 4. Generalized position and terms for macrosetae on the pronotum of adult Gyrophaenina (L = laterals; ML = mesolaterals; PM = paramedial; M = medials).



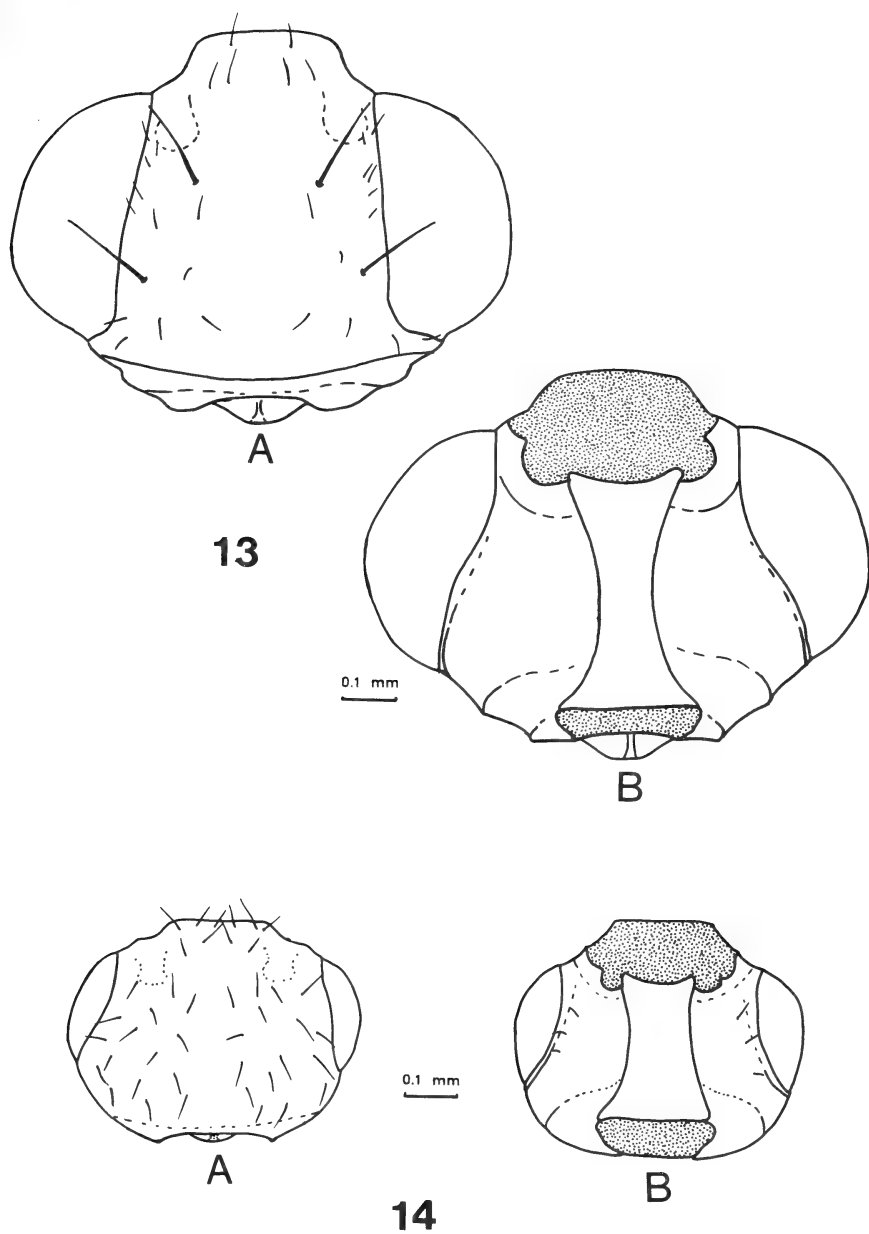




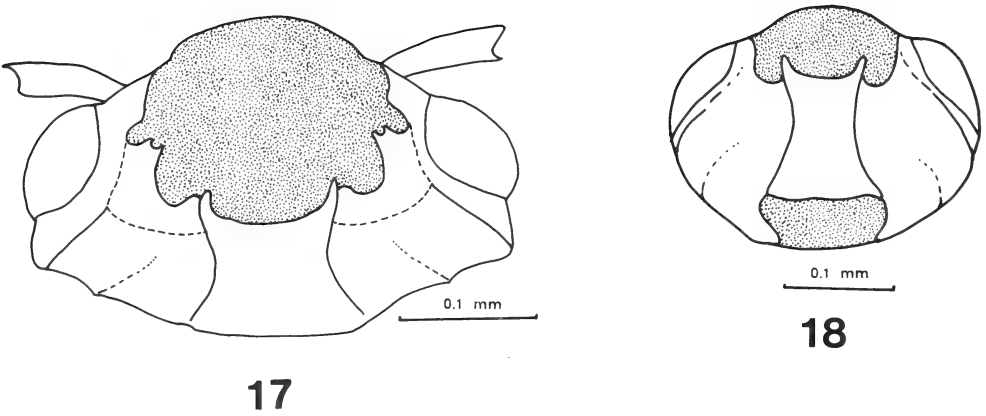
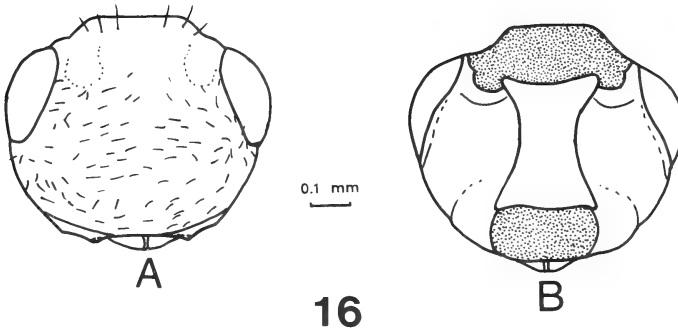
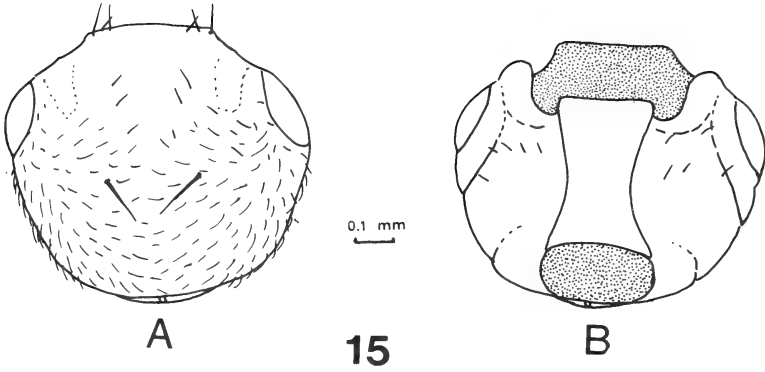
Figures 7-9. Illustrations of heads of adult Gyrophaenina. Fig. 7. *Gyrophaena nana* Payk., A) dorsal aspect, B) ventral aspect. Fig. 8. *Gyrophaena (Phaenogyra) gracilis* Seev., dorsal aspect. Fig. 9. *Gyrophaena sculptipennis* Csy., A) dorsal aspect, B) ventral aspect.



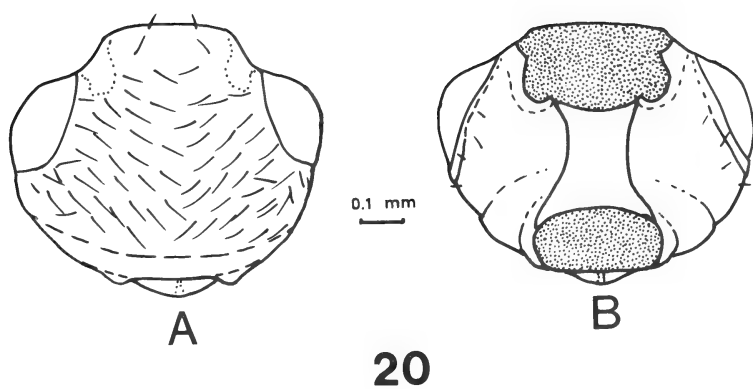
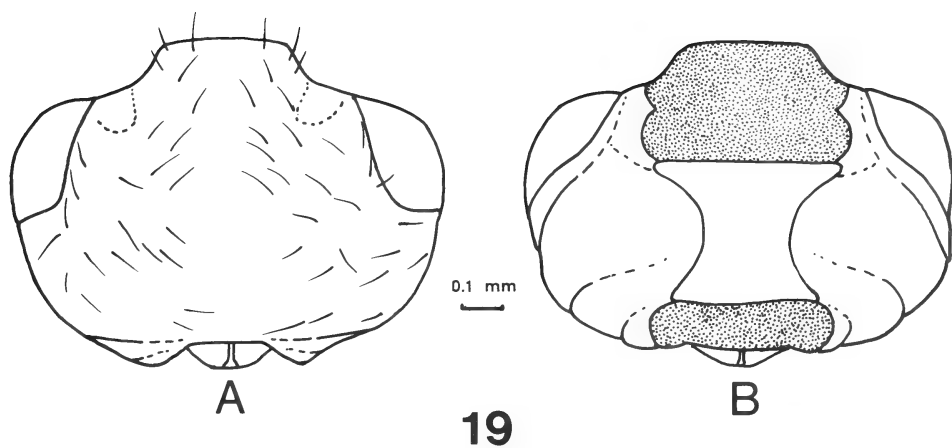
Figures 10-12. Illustrations of heads of adult Gyrophaenina. Fig. 10. *Gyrophaena egena* Csy., A) dorsal aspect, B) ventral aspect. Fig. 11. *Gyrophaena antennalis* Csy., A) dorsal aspect, B) ventral aspect. Fig. 12. *Phanerota fasciata* (Say), A) dorsal aspect, B) ventral aspect.



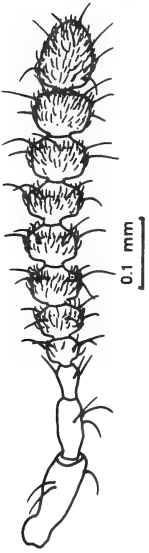
Figures 13-14. Illustrations of heads of adult Gyrophaenina. Fig. 13. *Phanerota (Acanthophaena) insigniventris* (Cam.), A) dorsal aspect, B) ventral aspect. Fig. 14. *Eumicrota corruscula* (Erichson), A) dorsal aspect, B) ventral aspect.



Figures 15-18. Illustrations of heads of adult Gyrophaenina. Fig. 15. *Brachida exigua* Heer., A) dorsal aspect, B) ventral aspect. Fig. 16. *Agaricochara laevicollis* Kr., A) dorsal aspect, B) ventral aspect. Fig. 17. *Sternotropa brevicornis* Cam., ventral aspect. Fig. 18. *Pseudoligota varians* Cam., ventral aspect.



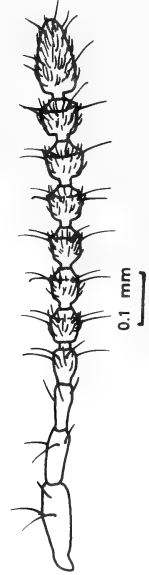
Figures 19-20. Illustrations of heads of adult Gyrophaenina. Fig. 19. *Brachychara* sp. (prob. *B. crassa* Sharp), A) dorsal aspect, B) ventral aspect. Fig. 20. *Agaricomorpha apacheana* (Seev.), A) dorsal aspect, B) ventral aspect.



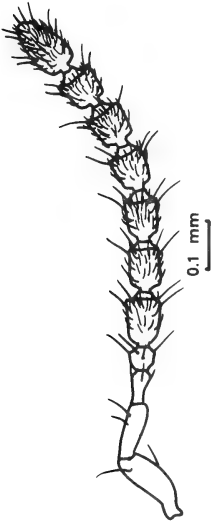
21



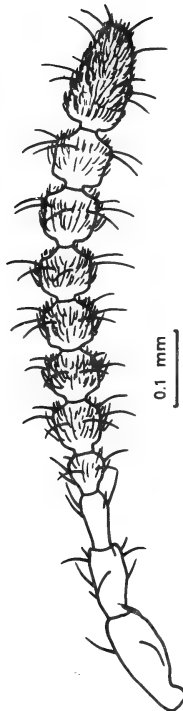
22



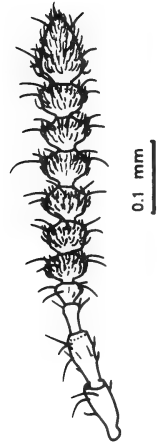
23



24

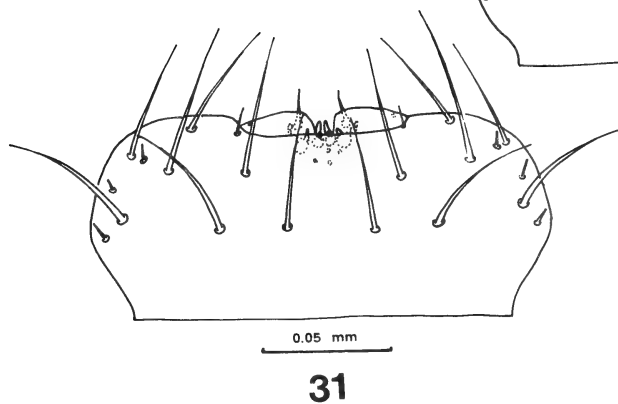
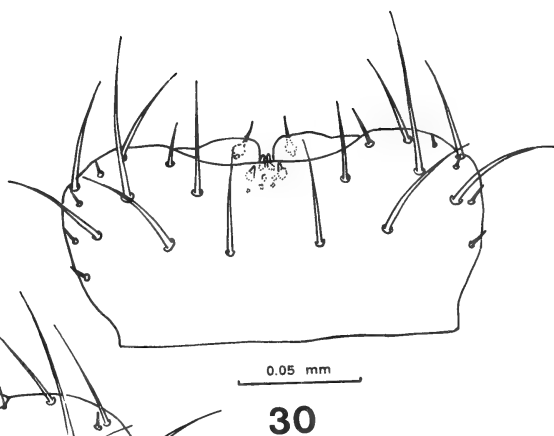
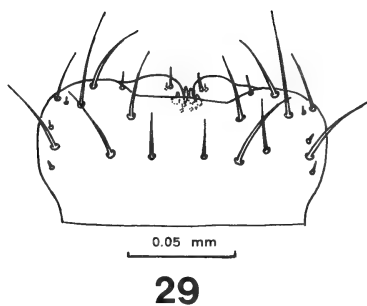
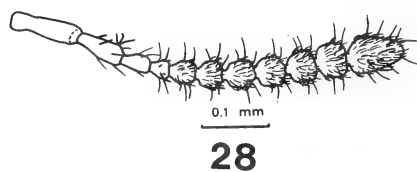
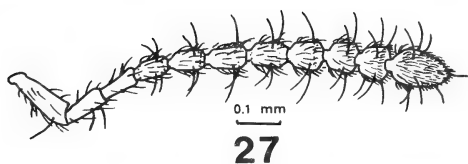


25



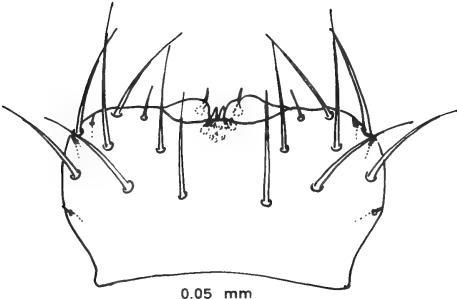
26

Figures 21-26. Illustrations of antennae of adult Gyrophaenina. Fig. 21. *Gyrophaena nana* Payk. Fig. 22. *Gyrophaena sculptipennis* Csy. Fig. 23. *Gyrophaena vitrina* Csy. Fig. 24. *Gyrophaena antennalis* Csy. Fig. 25. *Phanerota dissimilis* (Erichson). Fig. 26. *Eumicrota corruscula* (Erichson).

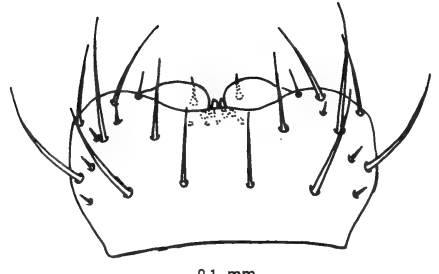


Figures 27-28. Illustrations of antennae of adult Gyrophaenina. Fig. 27. *Probrachida* undescr. sp. Fig. 28. *Agaricomorpha apacheana* (Seev.).

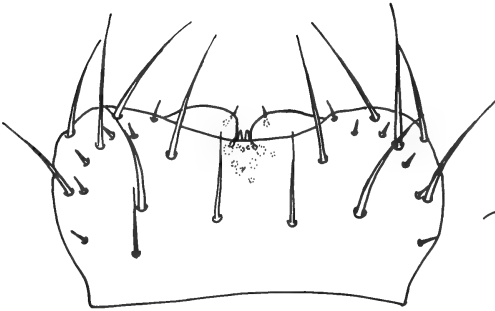
Figures 29-31. Illustrations of labra of adult Gyrophaenina. Fig. 29. *Gyrophaena affinis* Sahlb. Fig. 30. *Gyrophaena blackwelderi* Seev. Fig. 31. *Gyrophaena frosti* Seev.



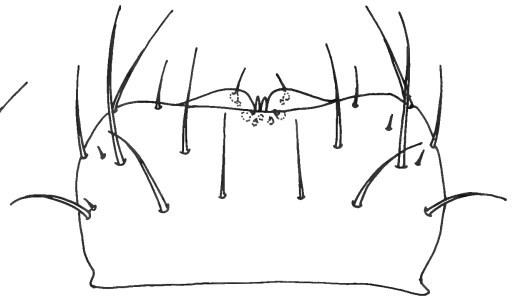
**32**



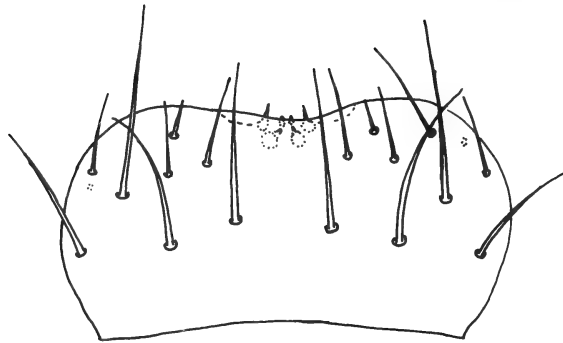
**33**



**34**



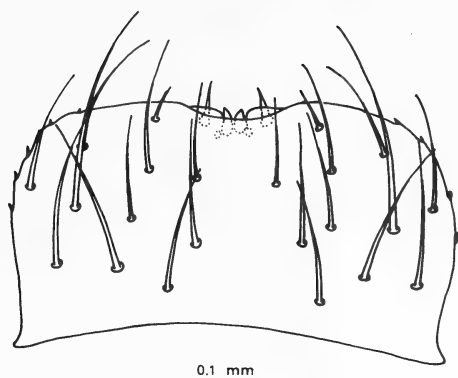
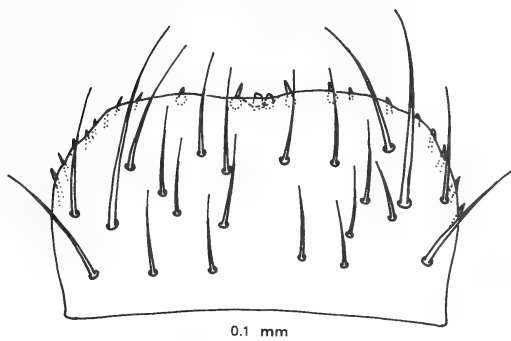
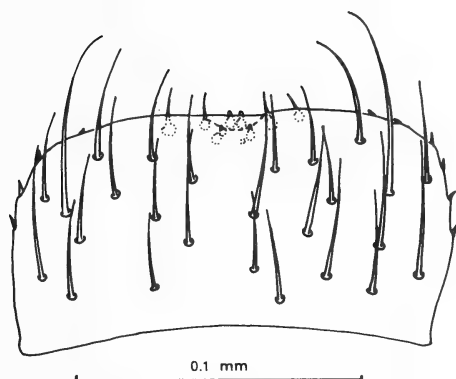
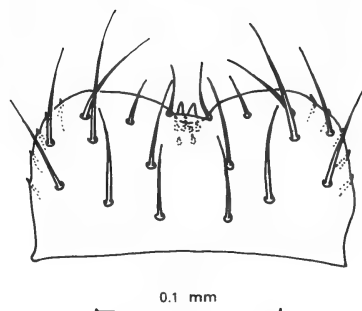
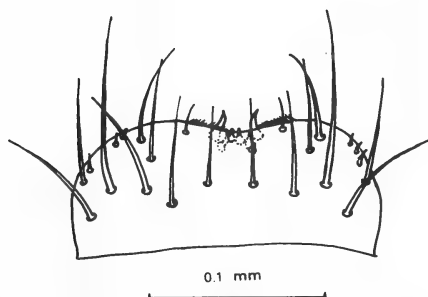
**35**



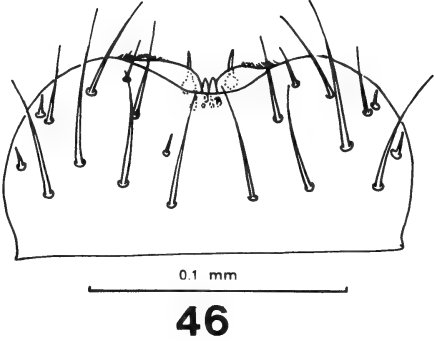
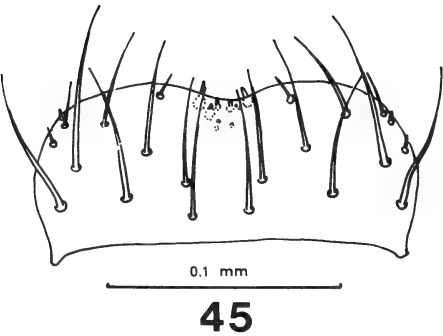
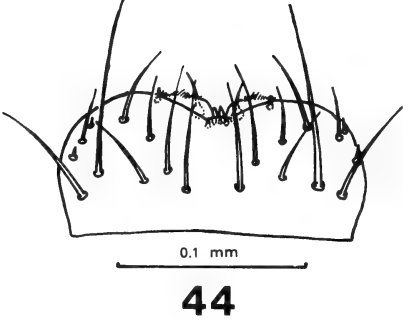
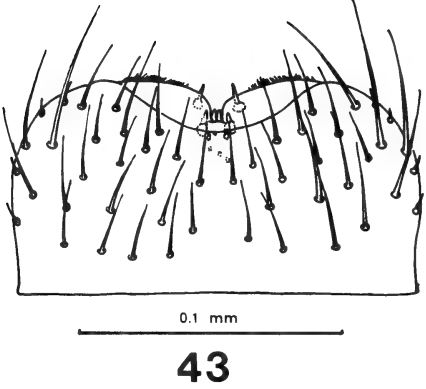
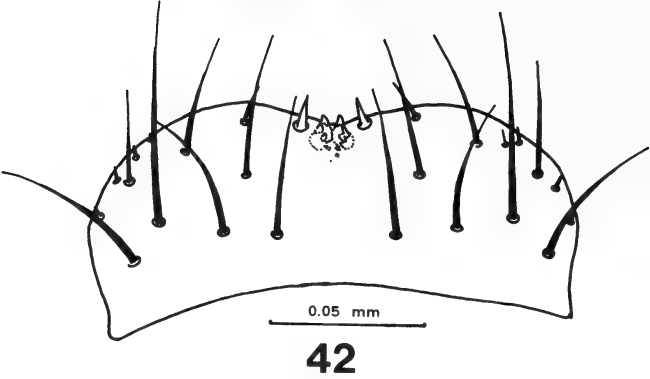
**36**

Figures 32-36. Illustrations of labra of adult Gyrophaenina. Fig. 32. *Gyrophaena antennalis* Csy. Fig. 33. *Phanerota fasciata* (Say). Fig. 34. *Phanerota dissimilis* (Erichson). Fig. 35. *Eumicrota corruscula* (Erichson). Fig. 36. *Encephalus americanus* Seev.

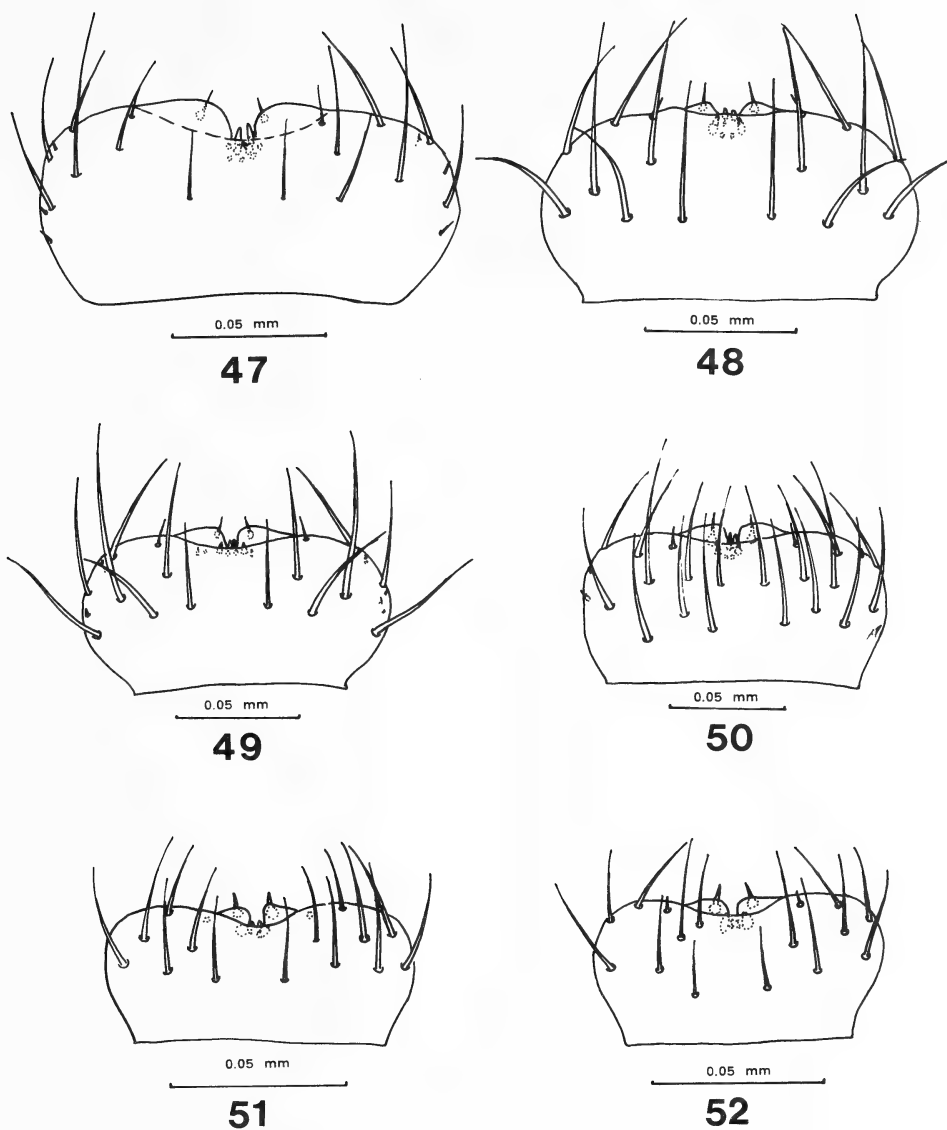


**37****38****39****40****41**

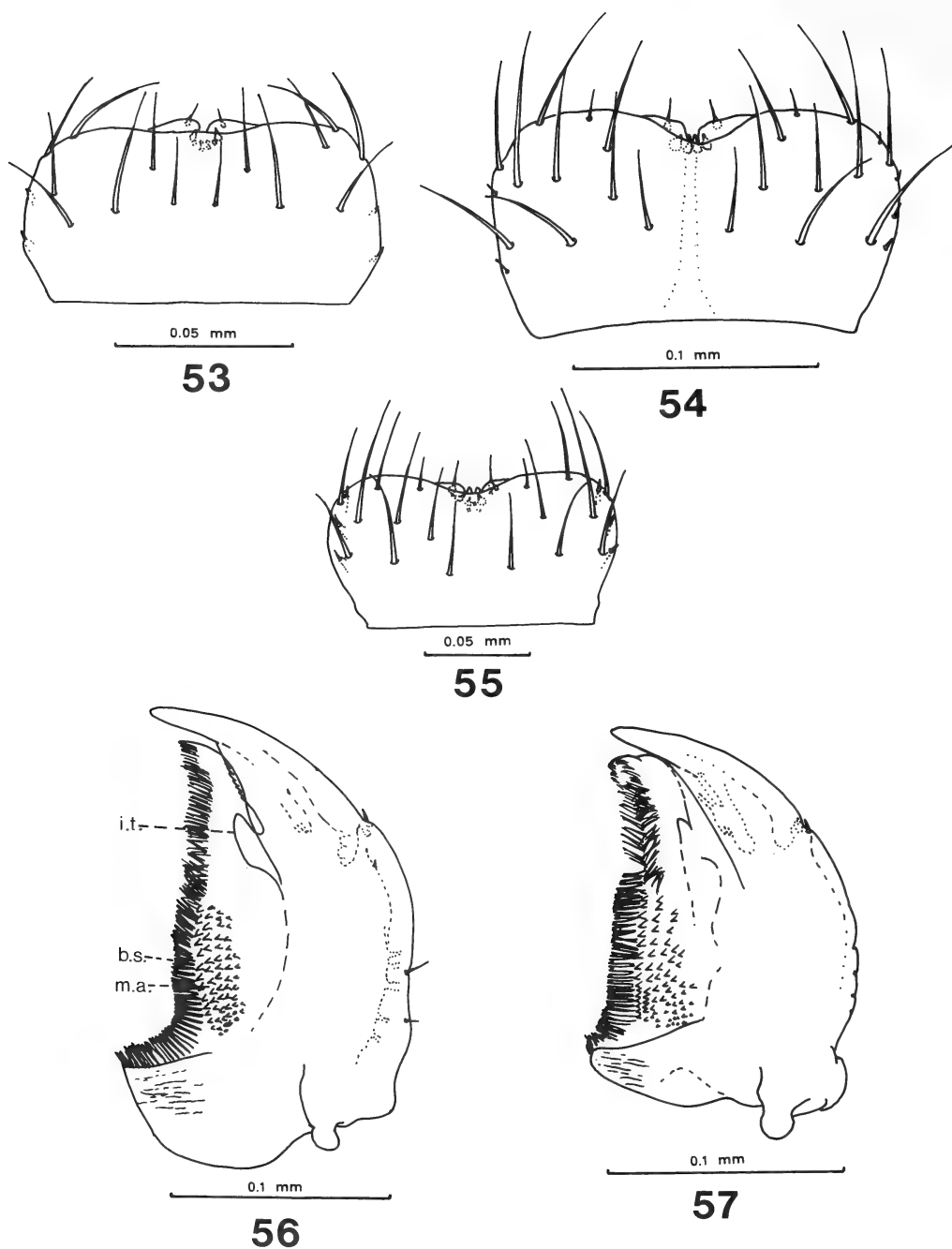
Figures 37-41. Illustrations of labra of adult Gyrophaenina. Fig. 37. *Probrachida modesta* (Sharp). Fig. 38. *Probrachida carinata* (Sharp). Fig. 39. *Probrachida sparsa* (Sharp). Fig. 40. *Probrachida geniculata* (Sharp). Fig. 41. *Probrachida undescr. sp.*



Figures 42-46. Illustrations of labra of adult Gyrophaenina. Fig. 42. *Brachida exigua* Heer. Fig. 43. *Brachida densiventris* Bernh. Fig. 44. *Brachida natalensis* Bernh. Fig. 45. *Brachida sublaevipennis* Cam. Fig. 46. *Brachida africana* Bernh.

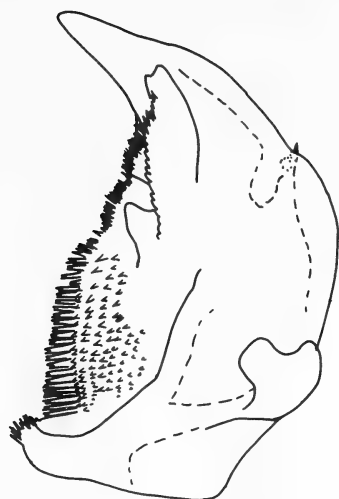


Figures 47-52. Illustrations of labra of adult Gyrophaenina. Fig. 47. *Agaricochara laevicollis* Kr. Fig. 48. *Sternotropa brevicornis* Cam. Fig. 49. *Sternotropa flavicornis* Cam. Fig. 50. *Sternotropa apicalis* Cam. Fig. 51. *Pseudoligota varians* Cam. Fig. 52. *Pseudoligota affinis* Cam.



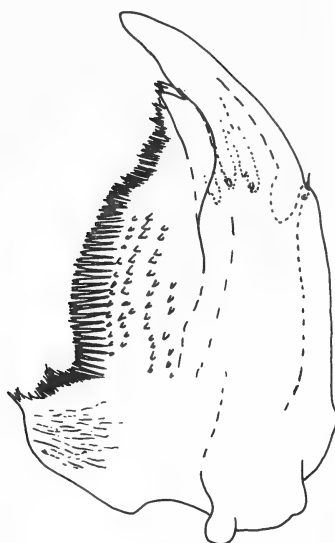
Figures 53-55. Illustrations of labra of adult Gyrophaenina. Fig. 53. *Adelarthra barbari* Cam. Fig. 54. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 55. *Agaricomorpha apacheana* (Seev.).

Figures 56-57. Illustrations of mandibles of adult Gyrophaenina. Fig. 56. *Gyrophaena vitrina* Csy., right. Fig. 57. *Phanerota fasciata* (Say), right.



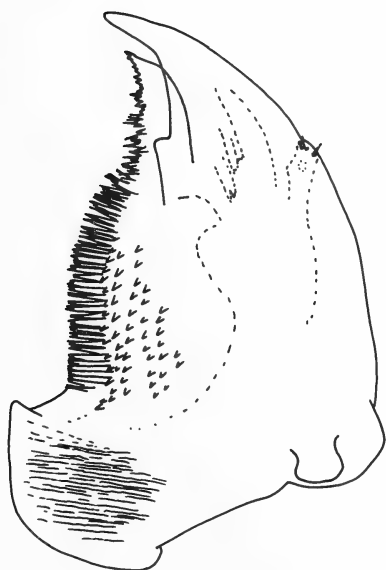
0.05 mm

58



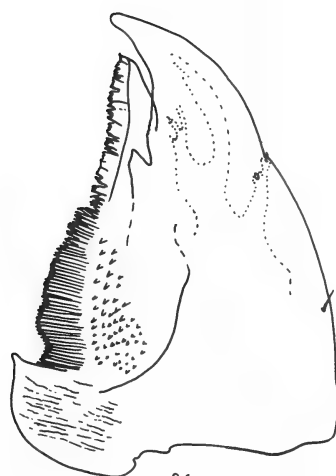
0.05 mm

59



0.1 mm

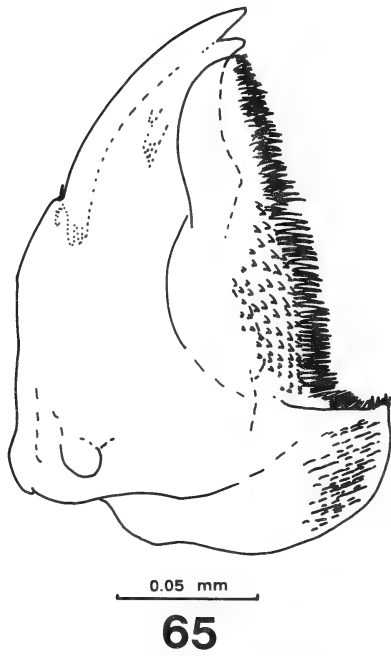
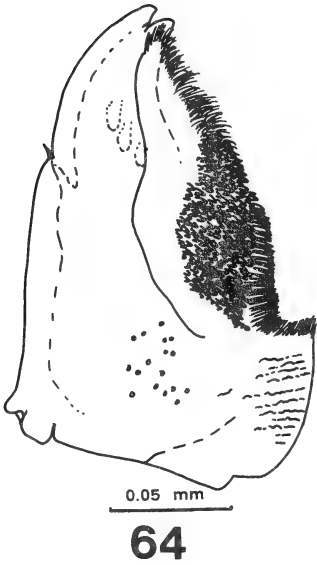
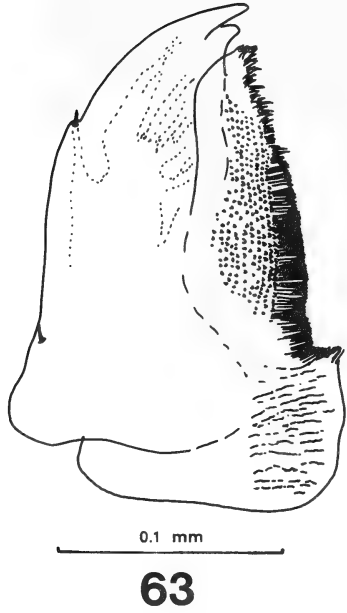
60



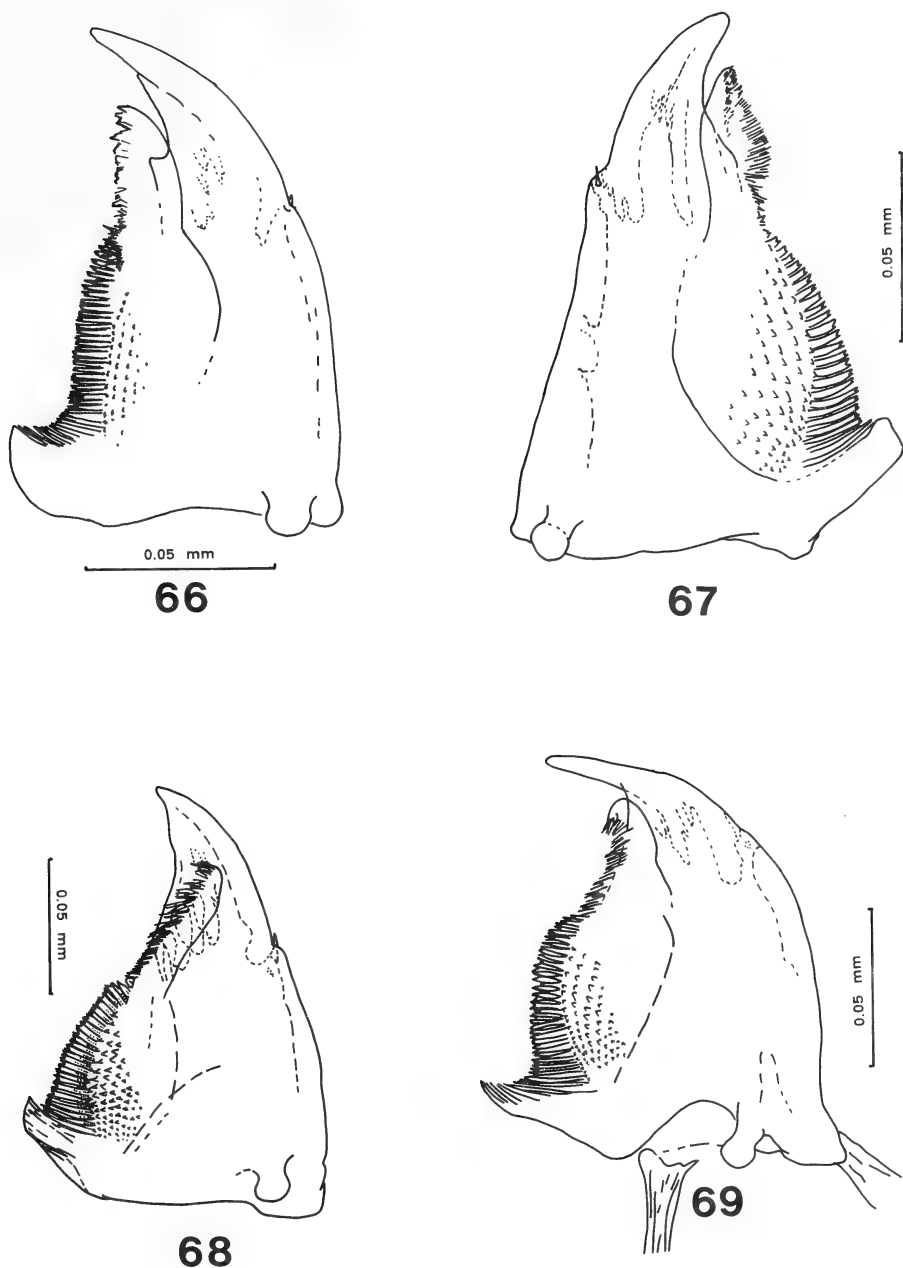
0.1 mm

61

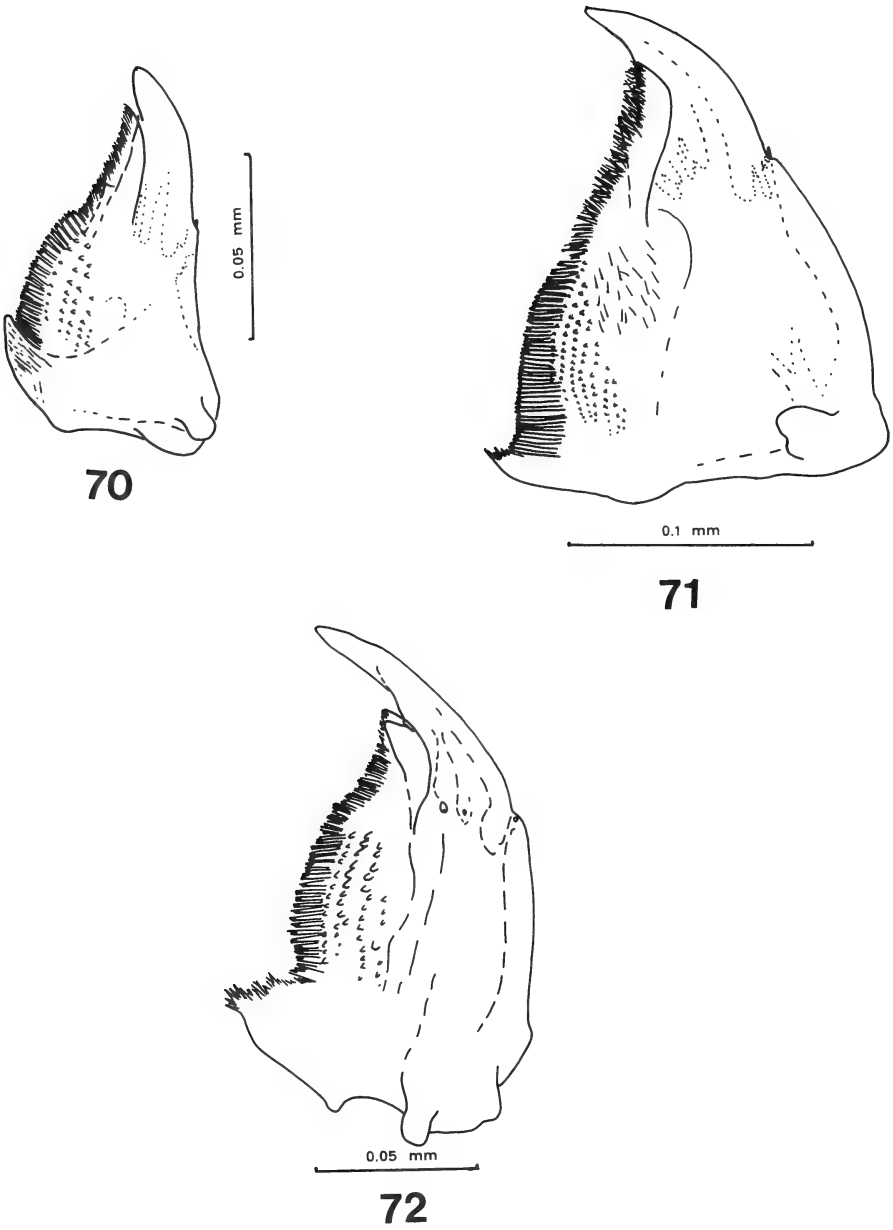
Figures 58-61. Illustrations of mandibles of adult Gyrophaenina. Fig. 58. *Phanerota (Acanthophaena) insigniventris* (Cam.), right. Fig. 59. *Eumicrota corruscula* (Erichson), right. Fig. 60. *Encephalus complicans* Kirby, right. Fig. 61. *Encephalus zealandicus* Cameron, right.



Figures 62-65. Illustrations of mandibles of adult Gyrophaenina. Fig. 62. *Probrachida modesta* (Sharp), left. Fig. 63. *Probrachida geniculata* (Sharp), left. Fig. 64. *Probrachida undescr. sp.*, left. Fig. 65. *Brachida exigua* Heer., left.

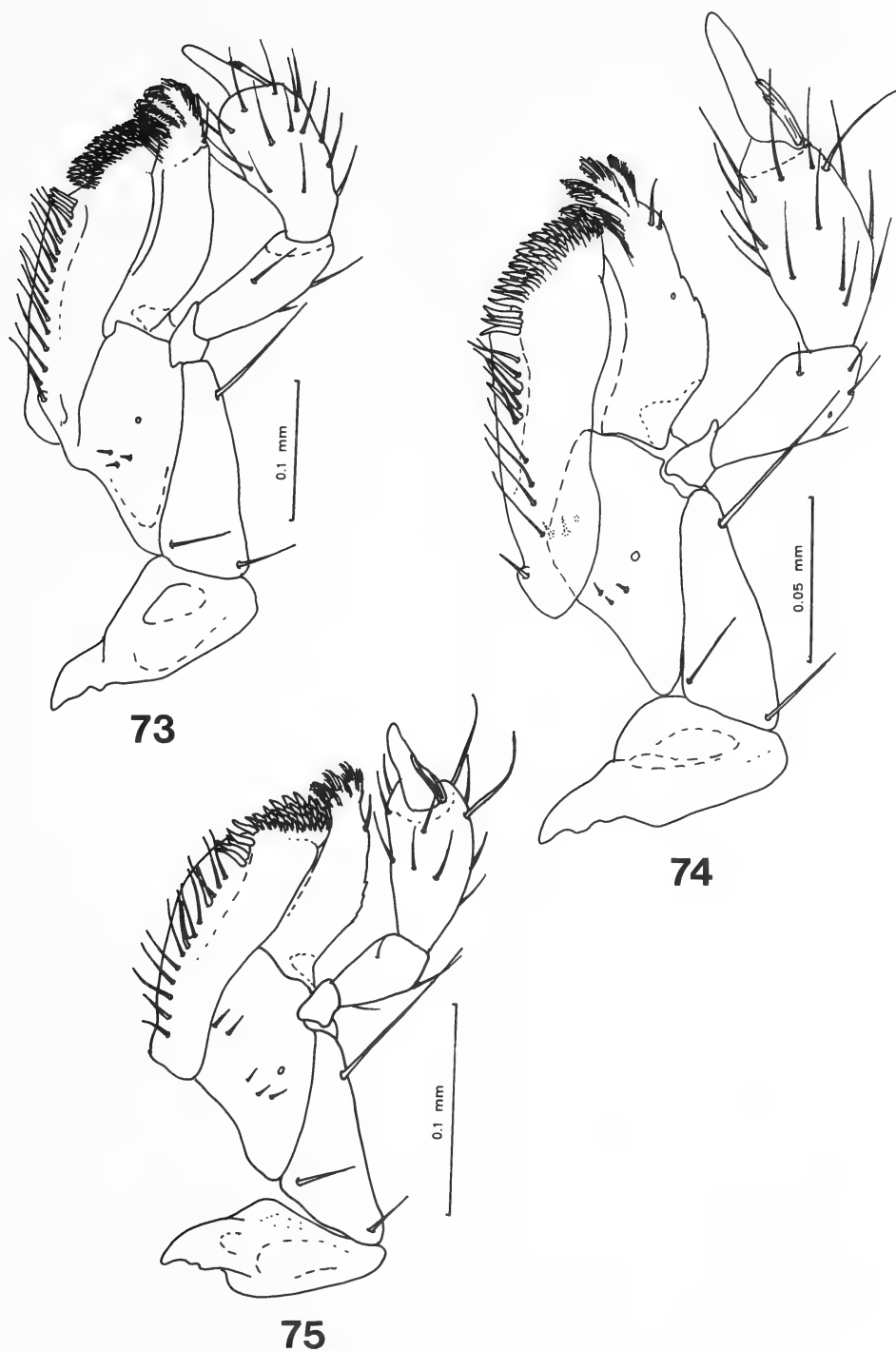


Figures 66-69. Illustrations of mandibles of adult Gyrophaenina. Fig. 66. *Agaricochara laevicollis* Kr., right. Fig. 67. *Sternotropa brevicornis* Cam., left. Fig. 68. *Sternotropa flavicornis* Cam., right. Fig. 69. *Sternotropa apicalis* Cam., right.

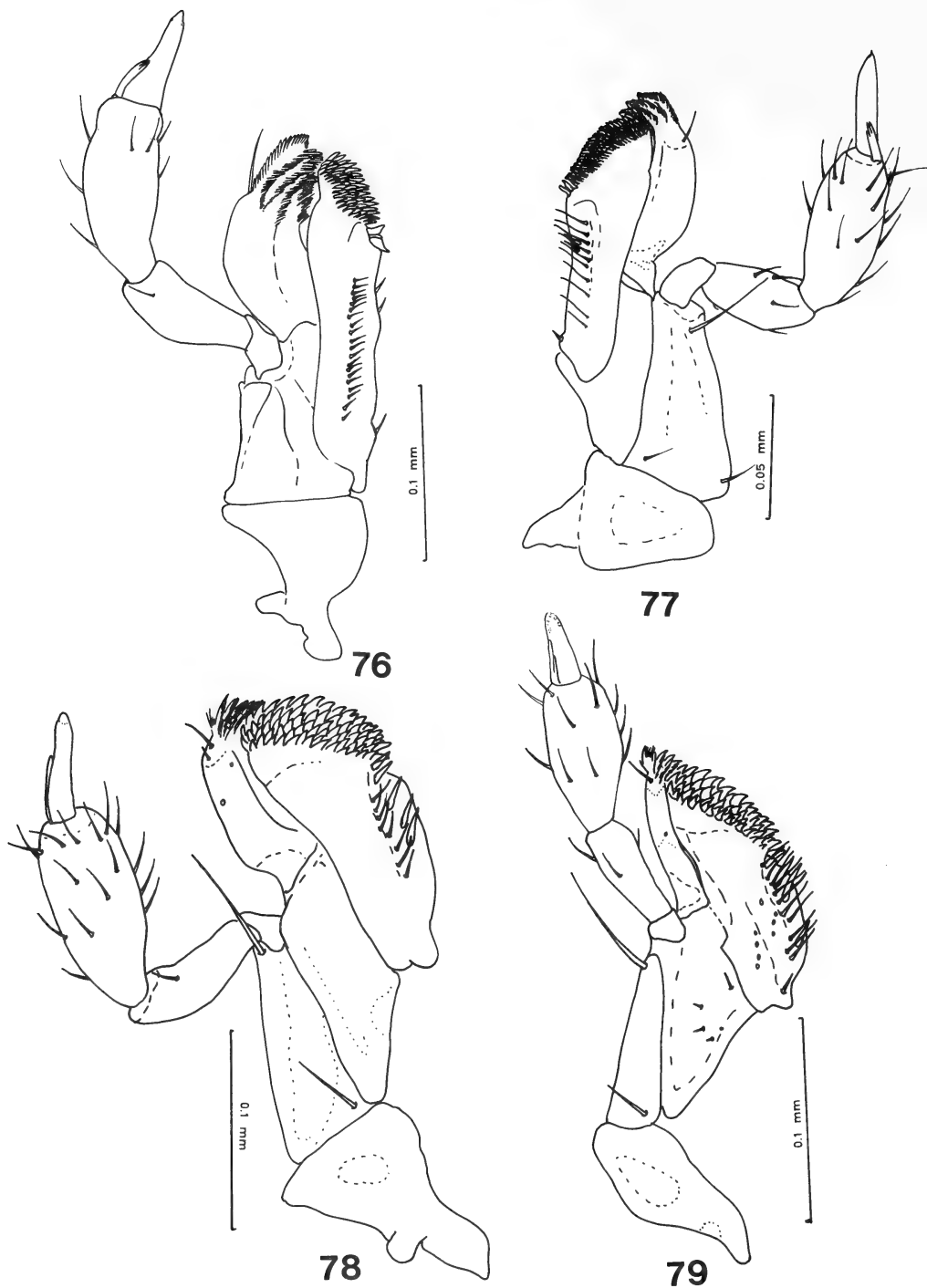


Figures 70-72. Illustrations of mandibles of adult Gyrophaenina. Fig. 70. *Pseudoligota affinis* Cam., right. Fig. 71. *Brachychara* sp. (prob. *B. crassa* Sharp), right. Fig. 72. *Agaricomorpha apacheana* (Seev.), right.

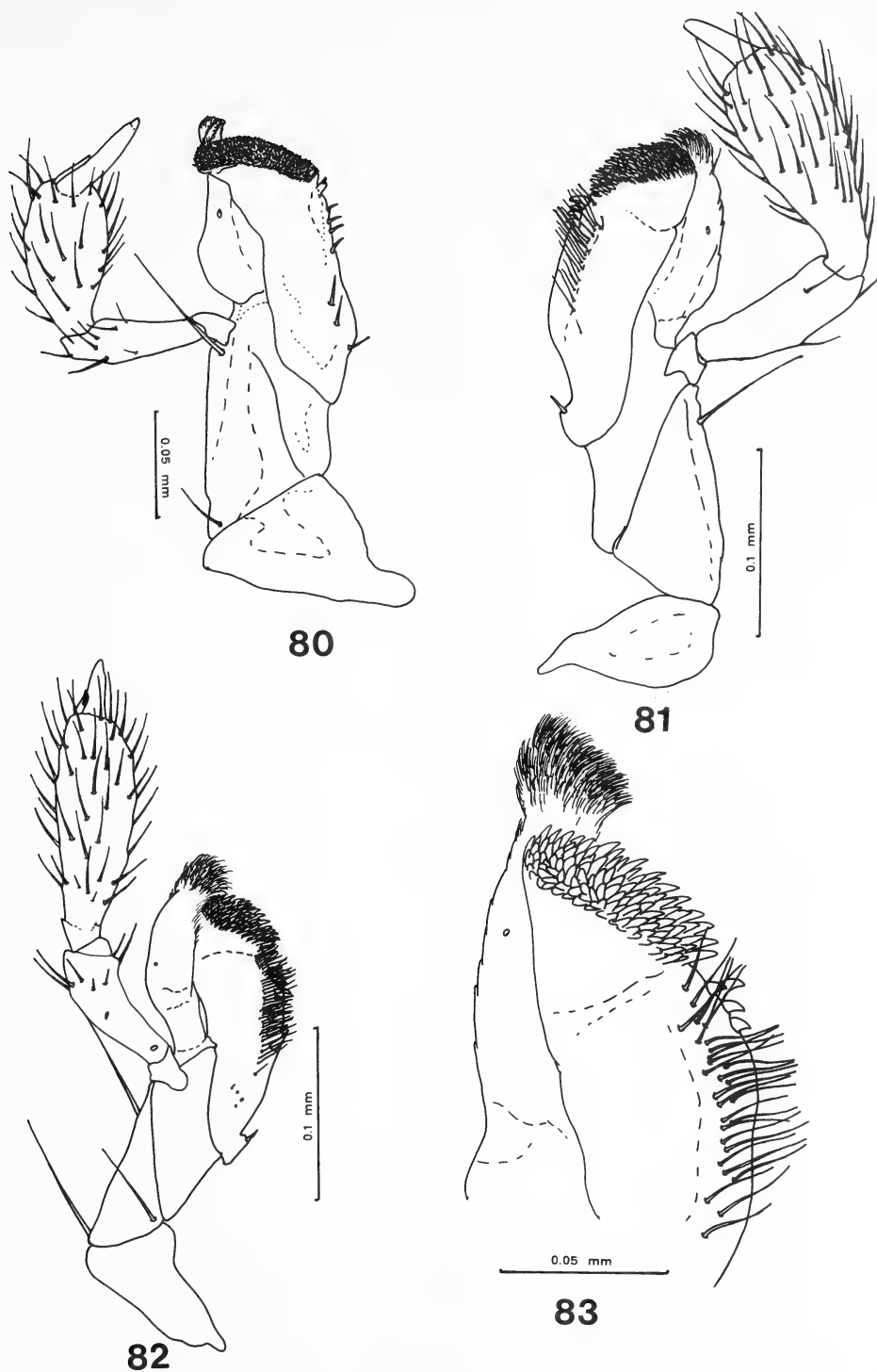




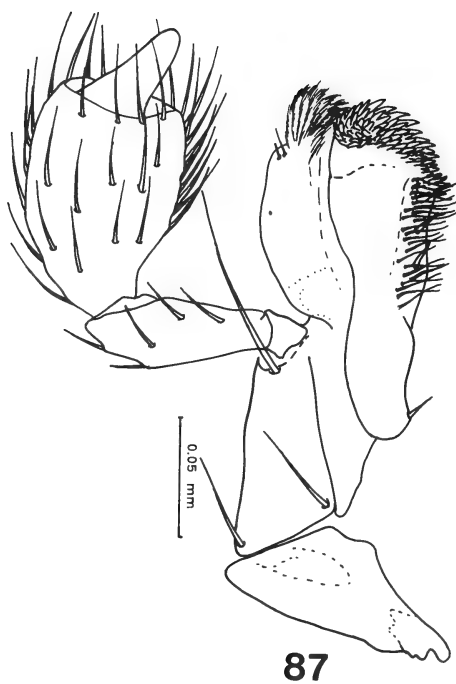
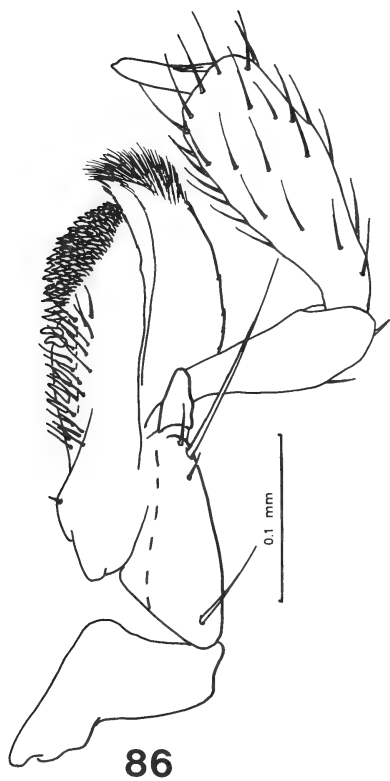
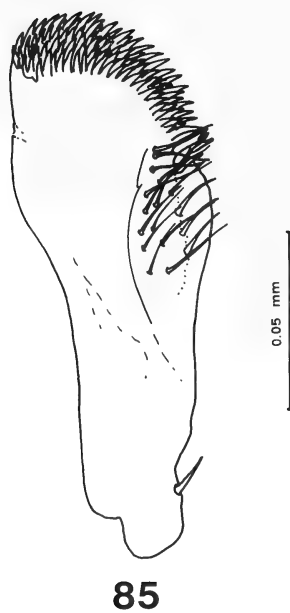
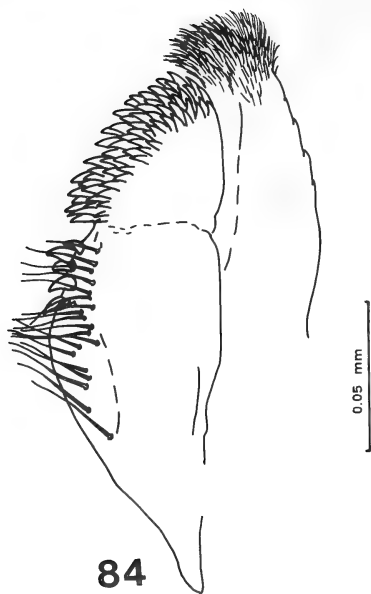
Figures 73-75. Illustrations of maxillae of adult Gyrophaenina. Fig. 73. *Gyrophaena antennalis* Csy. Fig. 74. *Gyrophaena affinis* Sahlb. Fig. 75. *Phanerota fasciata* (Say).



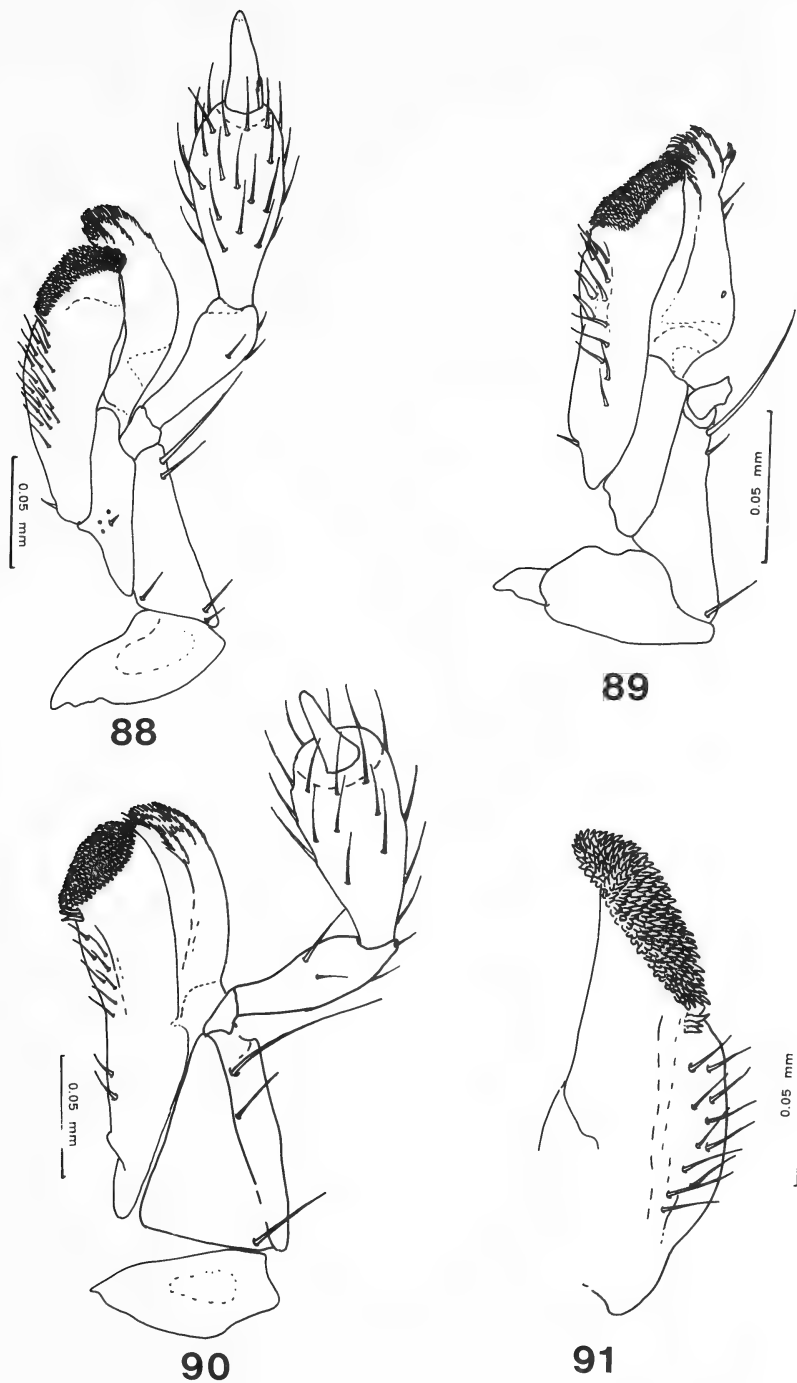
Figures 76-79. Illustrations of maxillae of adult Gyrophaenina. Fig. 76. *Phanerota (Acanthophaena) insigniventris* (Cam.) Fig. 77. *Eumicrota corruscula* (Erichson). Fig. 78. *Encephalus complicans* Kirby. Fig. 79. *Encephalus americanus* Seev.



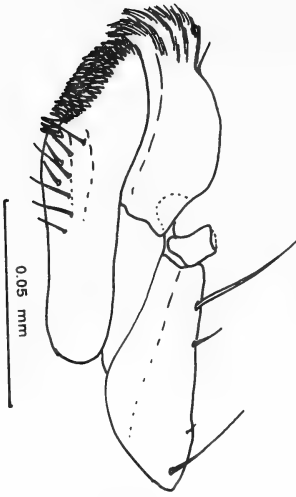
Figures 80-83. Illustrations of maxillae of adult Gyrophaenina. Fig. 80. *Encephalus zealandicus* Cameron. Fig. 81. *Probrachida modesta* (Sharp). Fig. 82. *Probrachida* undescr. sp. Fig. 83. *Probrachida sparsa* (Sharp), detail of galea and lacinia.



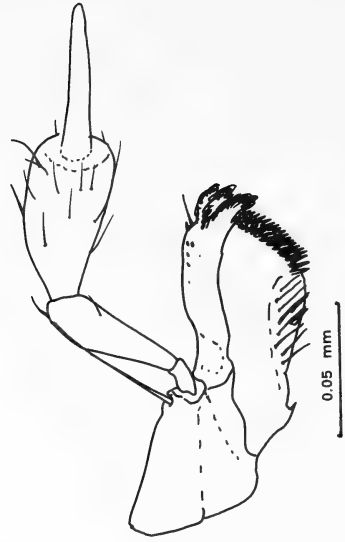
Figures 84-87. Illustrations of maxillae of adult Gyrophaenina. Fig. 84. *Probrachida carinata* (Sharp), detail of galea and lacinia. Fig. 85. *Brachida exigua* Heer., detail of lacinia. Fig. 86. *Brachida densiventris* Bernh. Fig. 87. *Brachida natalensis* Bernh.



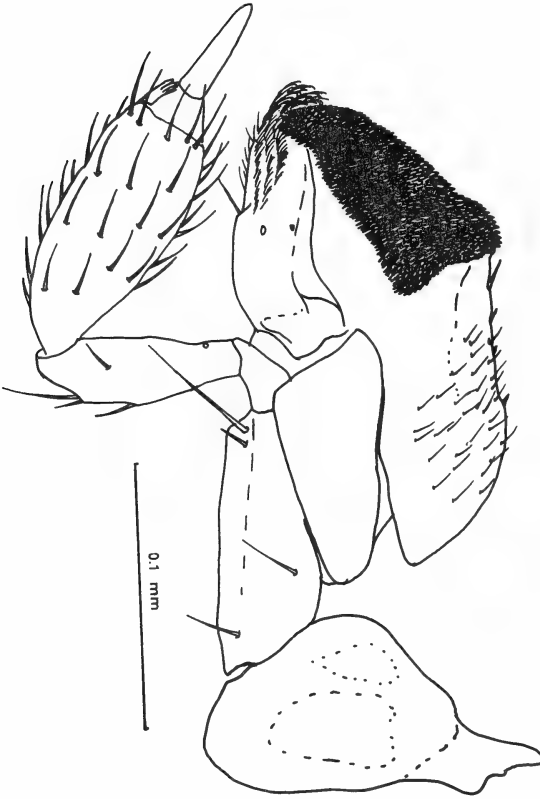
Figures 88-91. Illustrations of maxillae of adult Gyrophaenina. Fig. 88. *Agaricochara laevicollis* Kr. Fig. 89. *Sternotropa brevicornis* Cam. Fig. 90. *Sternotropa apicalis* Cam. Fig. 91. *Sternotropa apicalis* Cam., detail of lacinia.



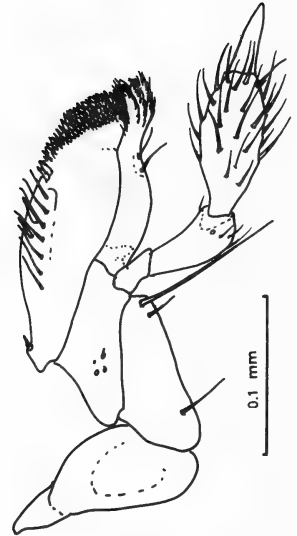
92



93

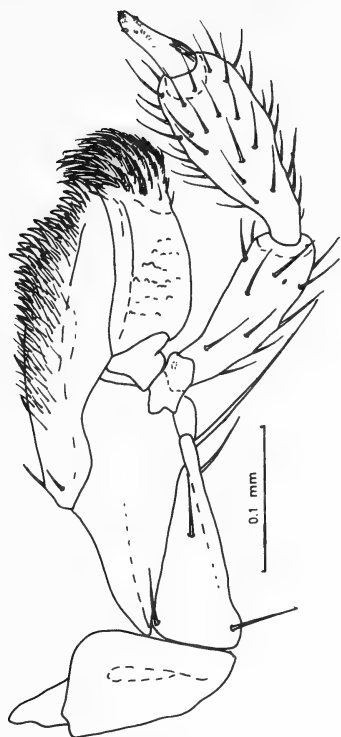


94



95

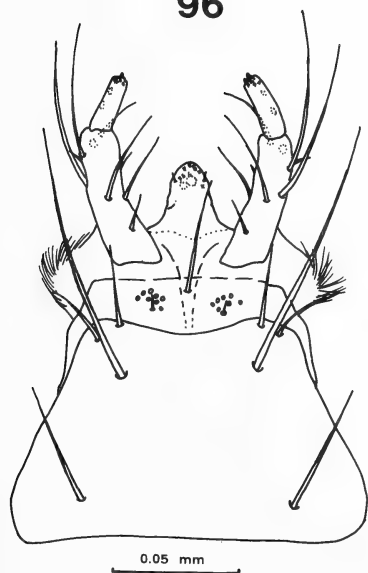
Figures 92-95. Illustrations of maxillae of adult Gyrophaenina. Fig. 92. *Pseudoligota affinis* Cam. Fig. 93. *Adelarthra barbari* Cam. Fig. 94. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 95. *Agaricomorpha apacheana* (Seev.).



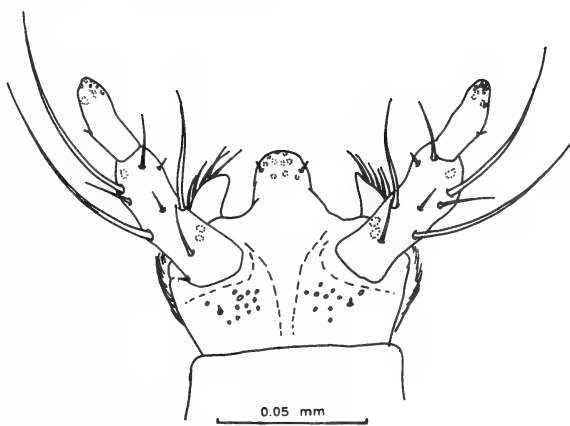
96



97



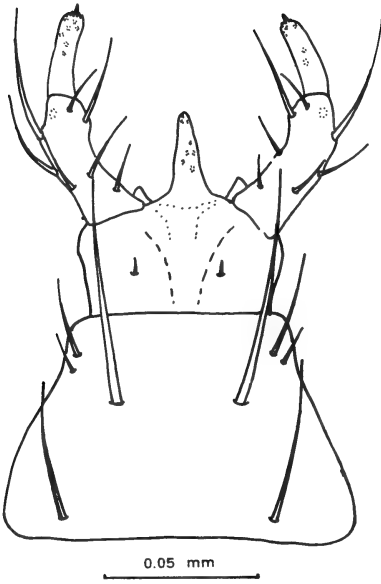
98



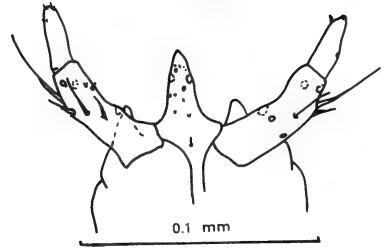
99

Figures 96-97. Illustrations of maxillae of adult Bolitocharina. Fig. 96. *Bolitochara lunulata* Gyll. Fig. 97. *Venusa* sp.

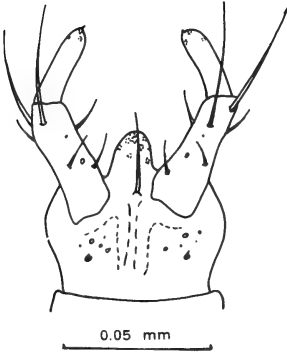
Figures 98-99. Illustrations of labia of adult Gyrophaenina. Fig. 98. *Gyrophaena antennalis* Csy. Fig. 99. *Gyrophaena vitrina* Csy.



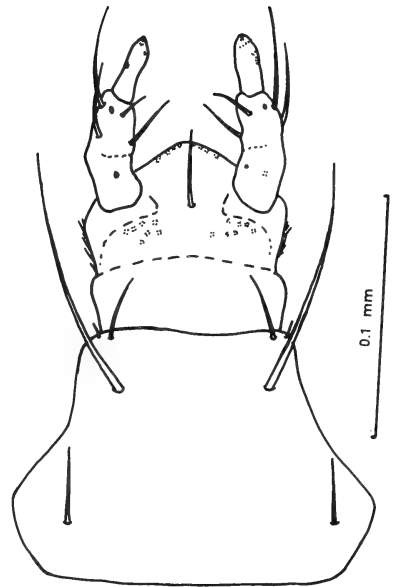
100



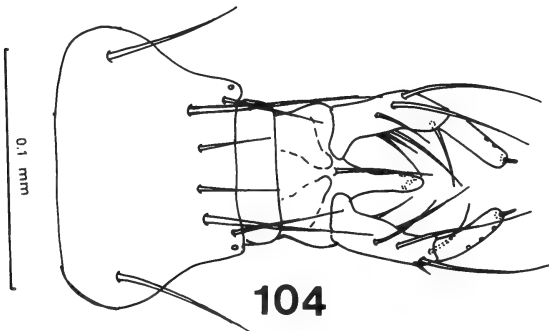
101



102



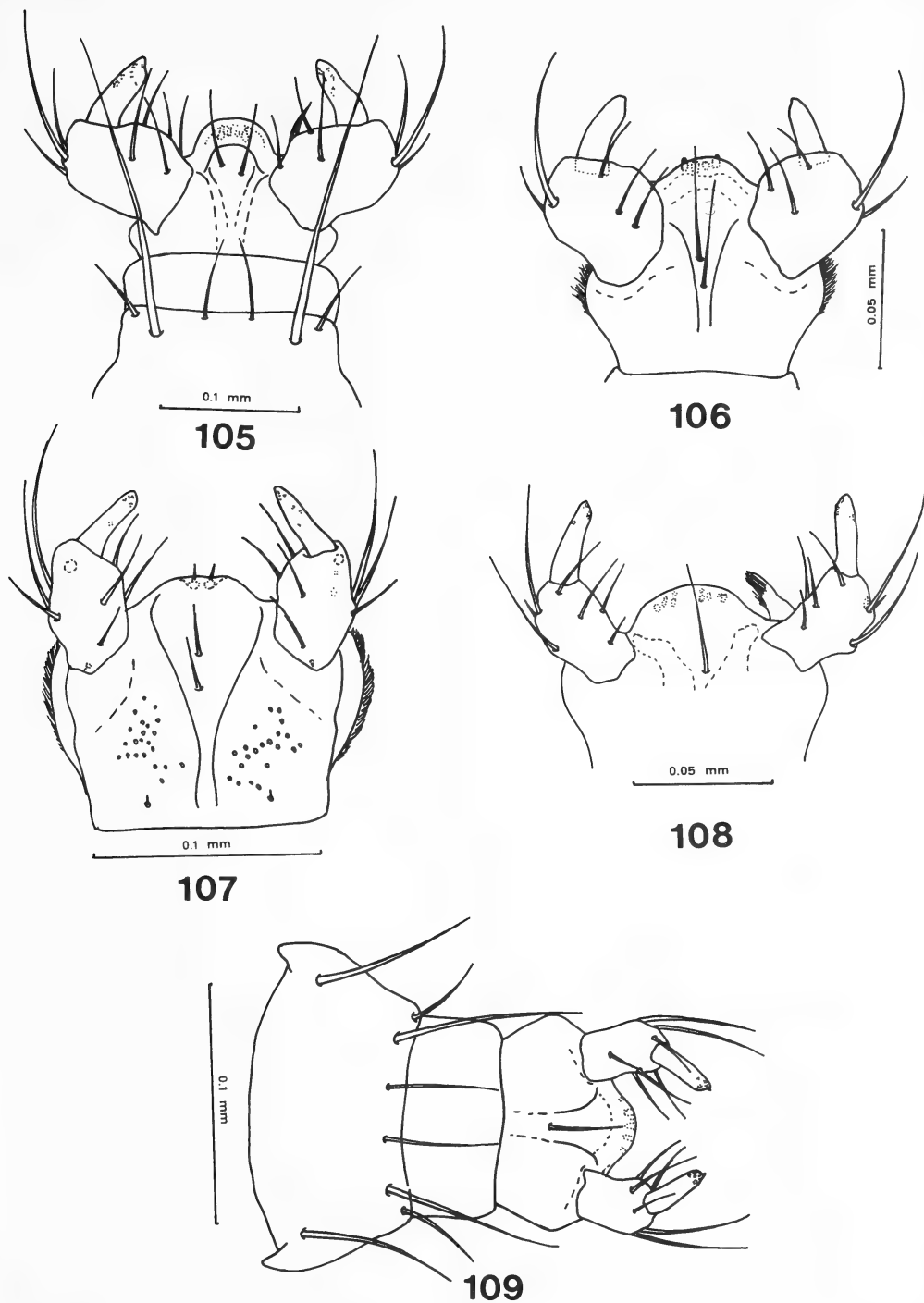
103



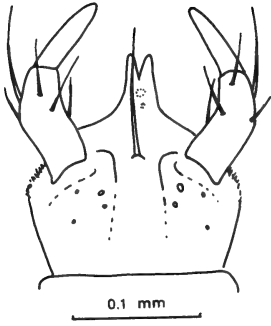
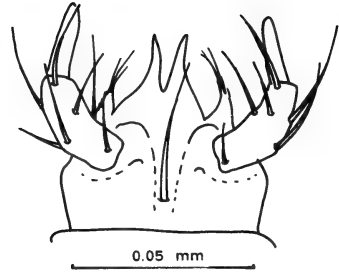
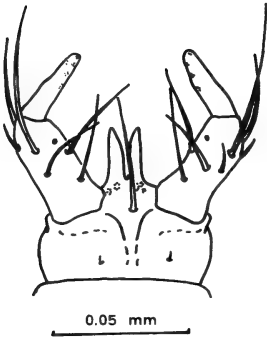
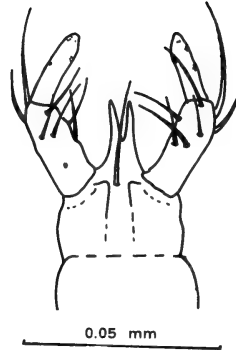
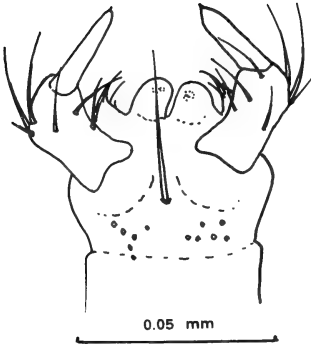
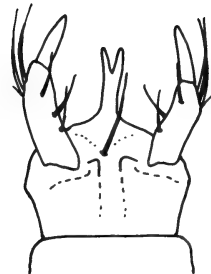
104

Figures 100-104. Illustrations of labia of adult Gyrophaenina. Fig. 100. *Phanerota fasciata* (Say). Fig. 101. *Phanerota* (*Acanthophaena*) *insigniventris* (Cam.) Fig. 102. *Eumicrota corruscula* (Erichson). Fig. 103. *Encephalus complicans* Kirby. Fig. 104. *Encephalus zealandicus* Cameron.

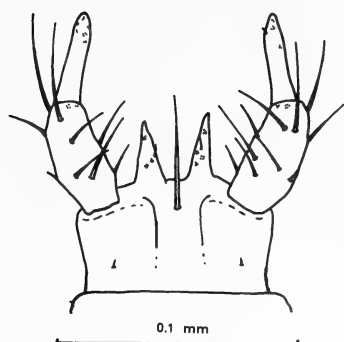




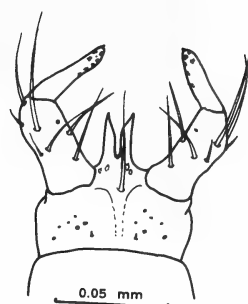
Figures 105-109 Illustrations of labia of adult Gyrophaenina. Fig. 105. *Probrachida modesta* (Sharp). Fig. 106. *Probrachida carinata* (Sharp). Fig. 107. *Probrachida* undescr. sp. Fig. 108. *Brachida exigua* Heer. Fig. 109. *Brachida africana* Bernh.

**110****111****112****113****114****115**

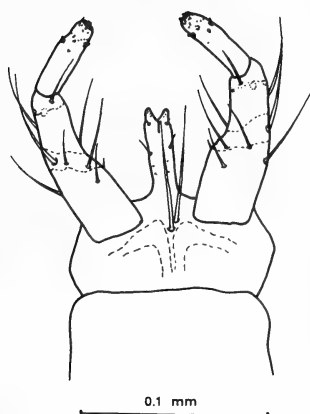
Figures 110-115 Illustrations of labia of adult Gyrophaenina. Fig. 110. *Agaricochara laevicollis* Kr. Fig. 111. *Sternotropa brevicornis* Cam. Fig. 112. *Sternotropa apicalis* Cam. Fig. 113. *Pseudoligota varians* Cam. Fig. 114. *Adelarthra barbari* Cam. Fig. 115. *Neobrachida castanea* Cam.



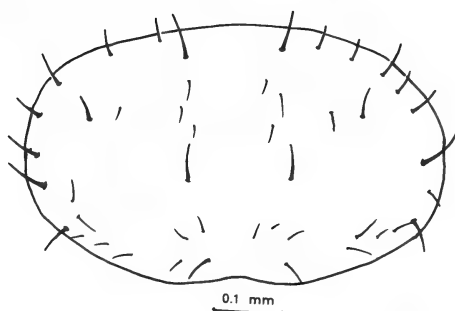
116



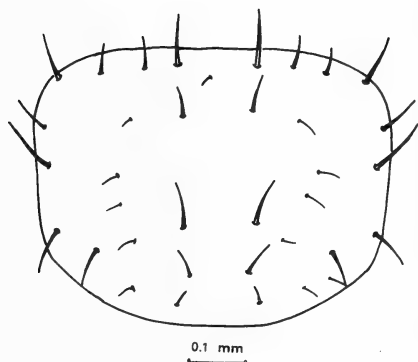
117



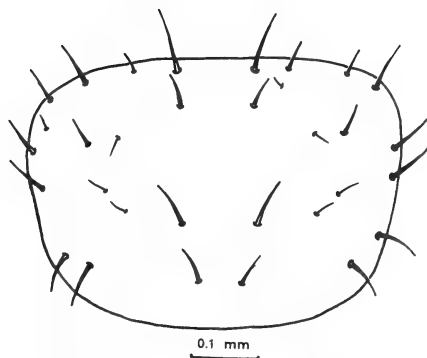
118



119



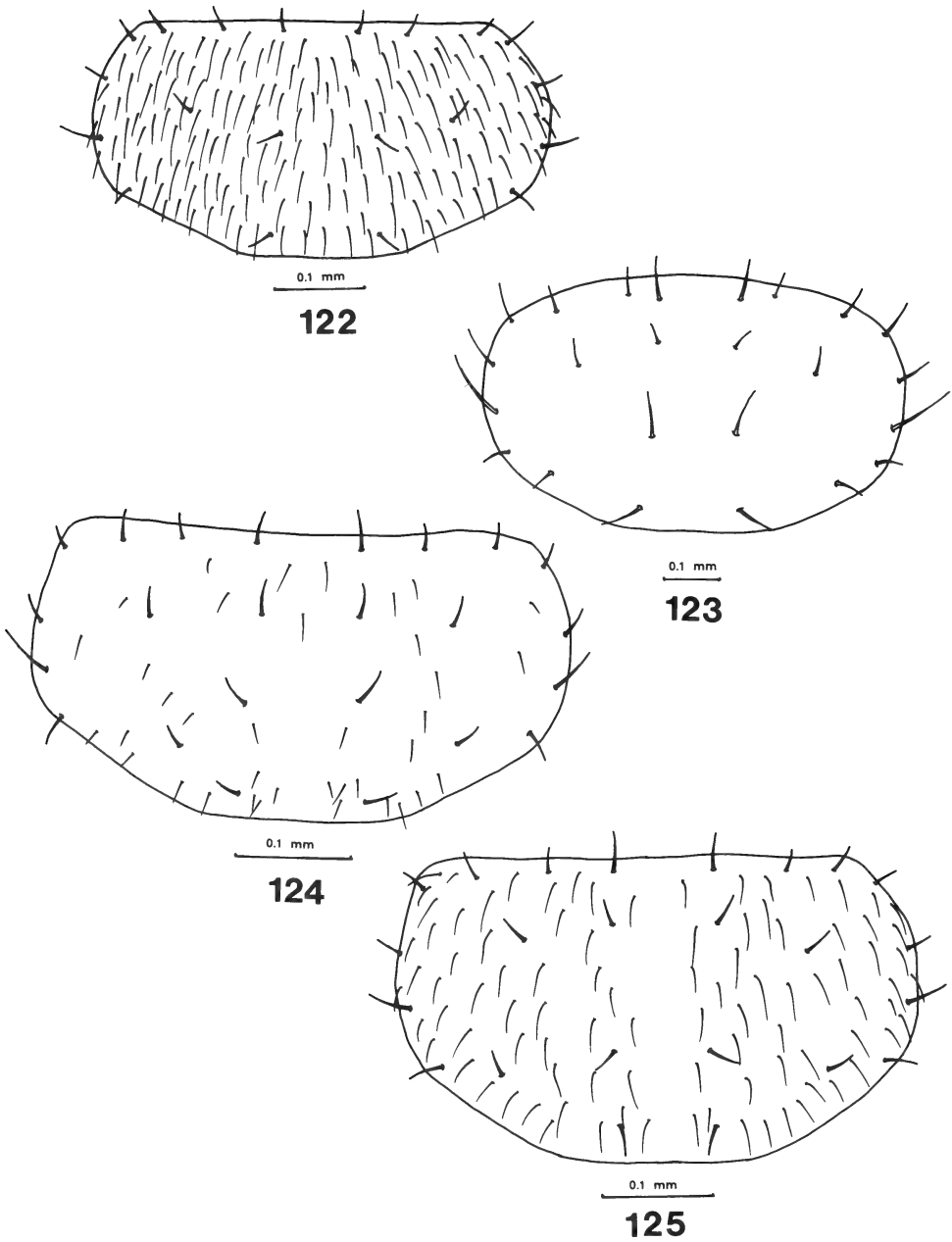
120



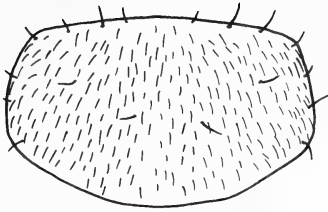
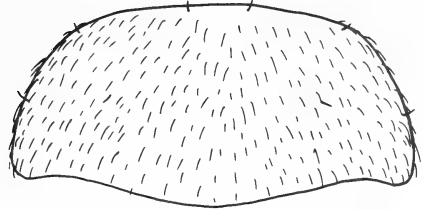
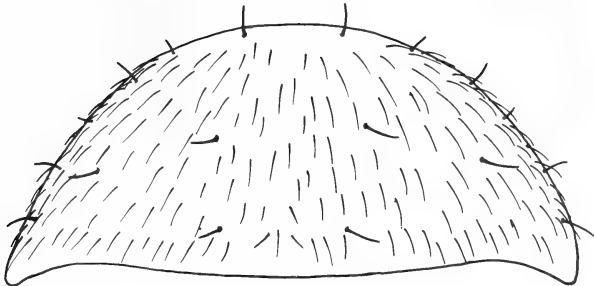
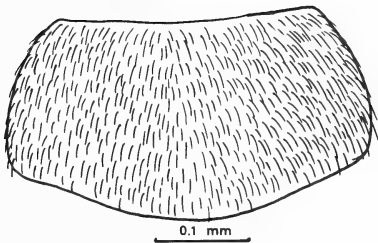
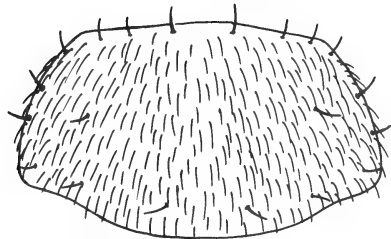
121

Figures 116-118. Illustrations of labia of adult Gyrophaenina and Bolitocharina. Fig. 116. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 117. *Agaricomorpha apacheana* (Seev.). Fig. 118. *Bolitochara lunulata* Gyll.

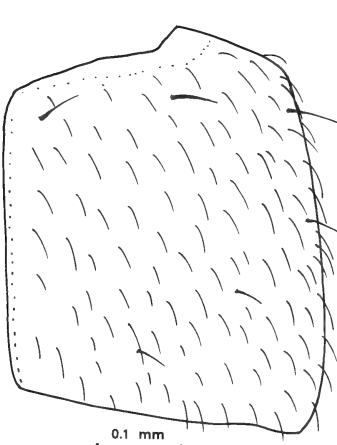
Figures 119-121. Illustrations of dorsal aspect of pronota of adult Gyrophaenina. Fig. 119. *Gyrophaena nana* Payk. Fig. 120. *Gyrophaena antennalis* Csy. Fig. 121. *Gyrophaena blackwelderi* Seev.



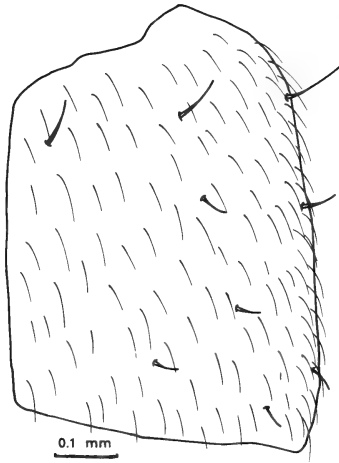
Figures 122-125. Illustrations of dorsal aspect of pronota of adult Gyrophaenina. Fig. 122. *Gyrophaena hubbardi* Seev. Fig. 123. *Phanerota dissimilis* (Erichson). Fig. 124. *Eumicrota corruscula* (Erichson). Fig. 125. *Eumicrota socia* (Erichson).

**126****127****129****128****130**

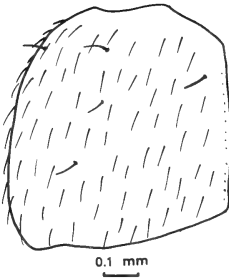
Figures 126-130. Illustrations of dorsal aspect of pronota of adult Gyrophaenina. Fig. 126. *Agaricochara laevicollis* Kr. Fig. 127. *Sternotropa brevicornis* Cam. Fig. 128. *Pseudoligota varians* Cam. Fig. 129. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 130. *Agaricomorpha apacheana* (Seev.).



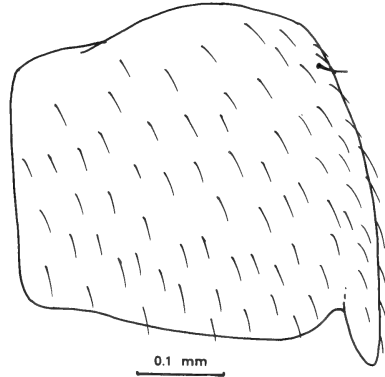
**131**



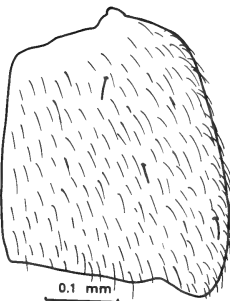
**132**



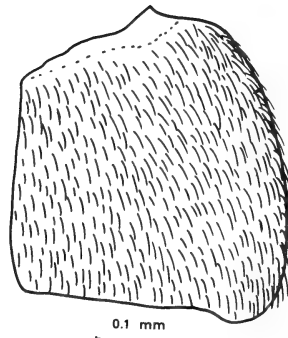
**133**



**134**

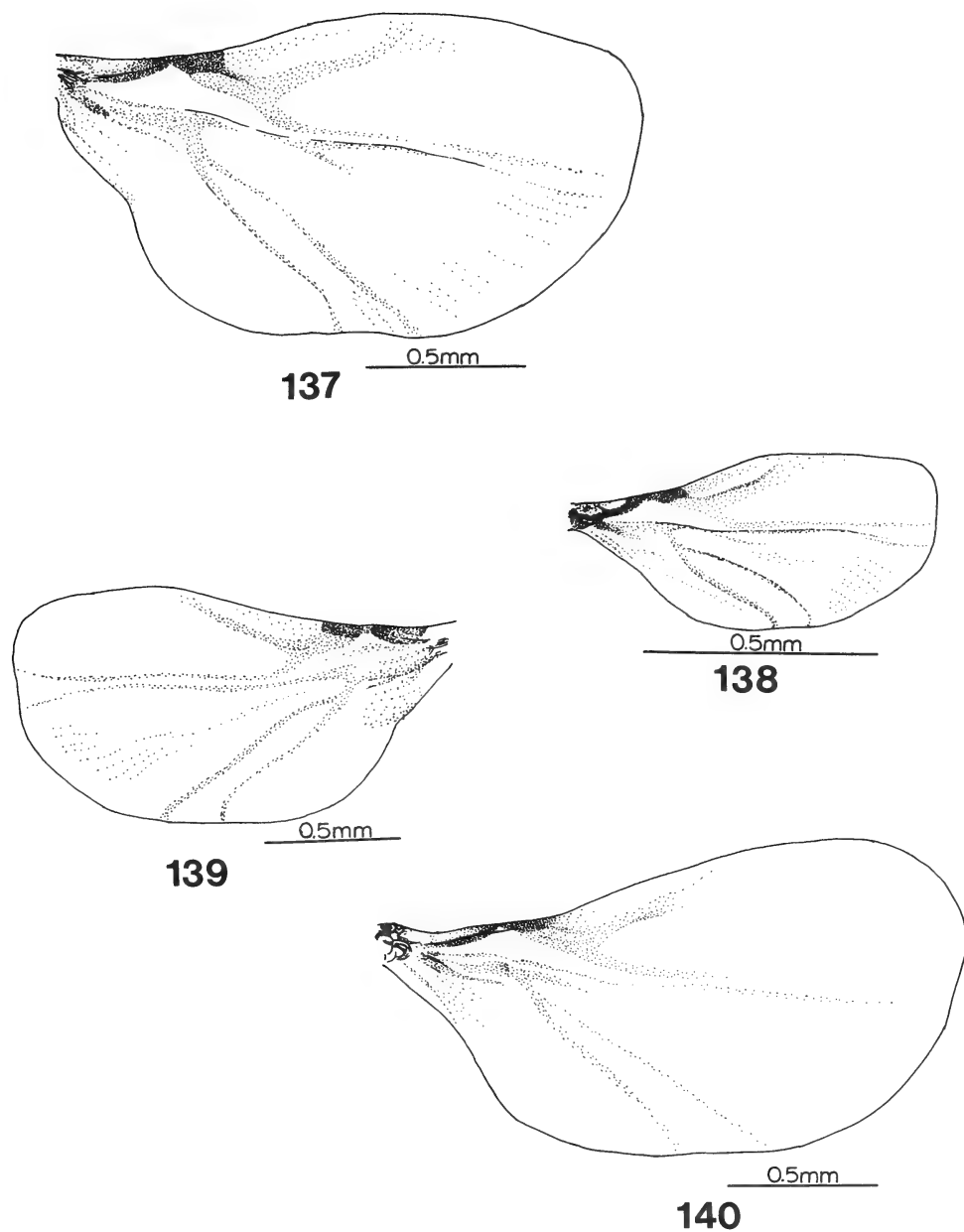


**135**



**136**

Figures 131-136. Illustrations of dorsal aspect of elytra of adult Gyrophaenina. Fig. 131. *Gyrophaena nana* Payk. Fig. 132. *Phanerota dissimilis* (Erichson). Fig. 133. *Eumicrota corruscula* (Erichson). Fig. 134. *Encephalus zealandicus* Cameron. Fig. 135. *Sternotropa elevata* (Fvl.). Fig. 136. *Pseudoligota varians* Cam.



Figures 137-140. Illustrations of wings of adult Gyrophaenina. Fig. 137. *Gyrophaena nana* Payk. Fig. 138. *Phanerota fasciata* (Say). Fig. 139. *Eumicrota corruscula* (Erichson). Fig. 140. *Agaricomorpha apacheana* (Seev.).

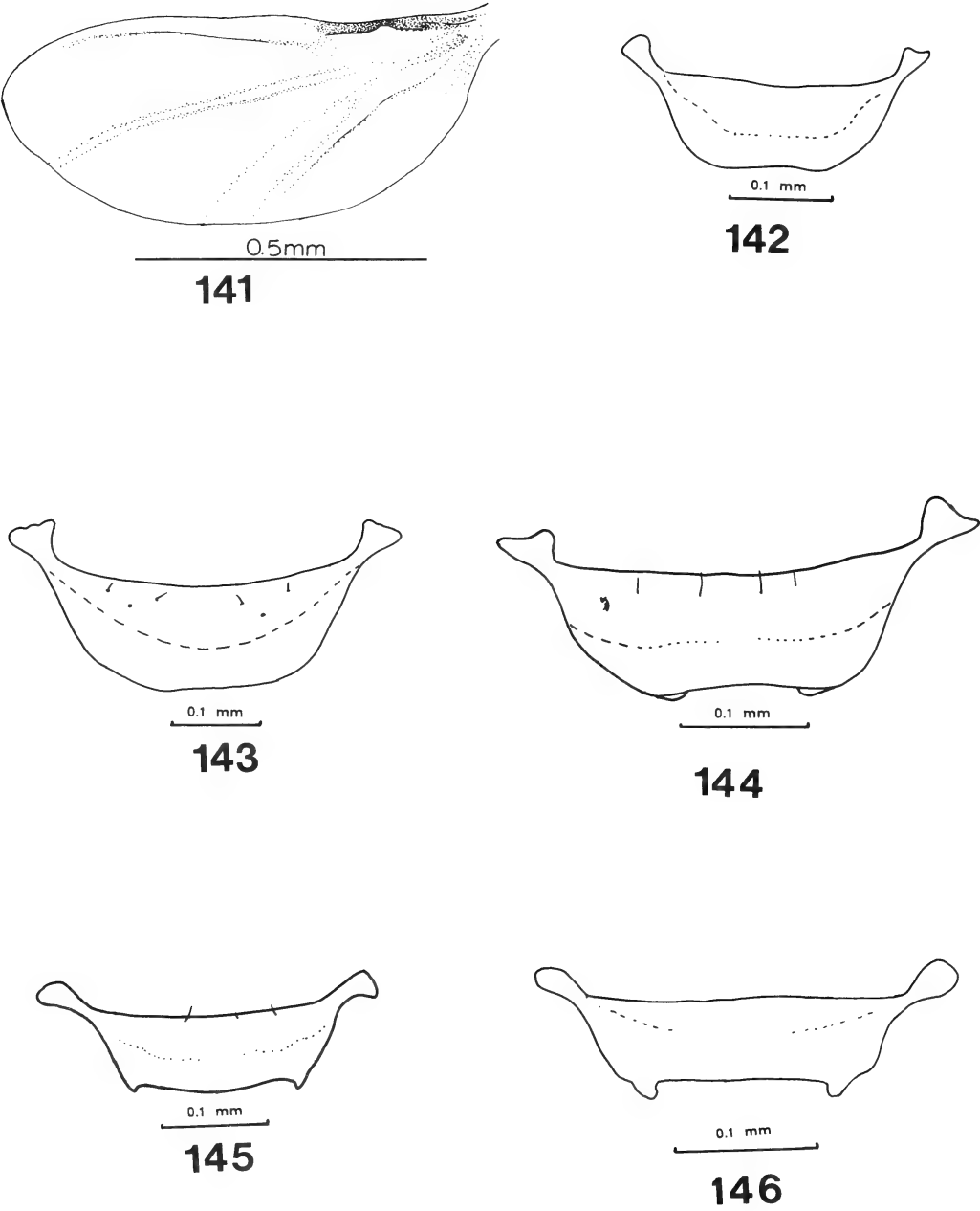
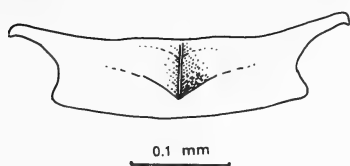
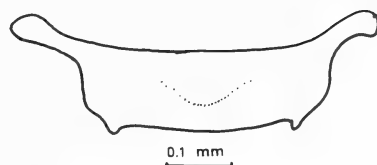


Figure 141. Illustration of wing of members of *Venusa* sp. (subtribe Bolitocharina).  
Figures 142-146. Illustrations of prosterna of adult Gyrophaenina. Fig. 142. *Gyrophaena affinis* Sahlb. Fig. 143. *Gyrophaena frosti* Seev. Fig. 144. *Phanerota fasciata* (Say). Fig. 145. *Eumicrota corruscula* (Erichson). Fig. 146. *Agaricochara laevicollis* Kr.

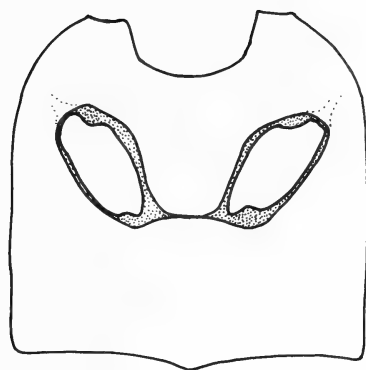




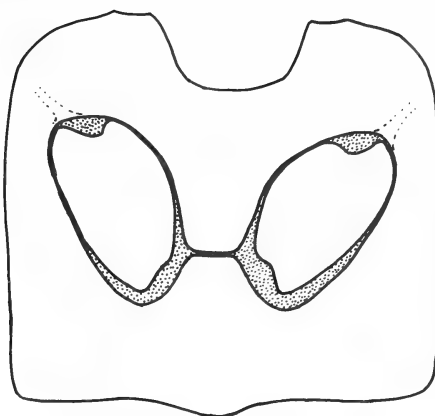
147



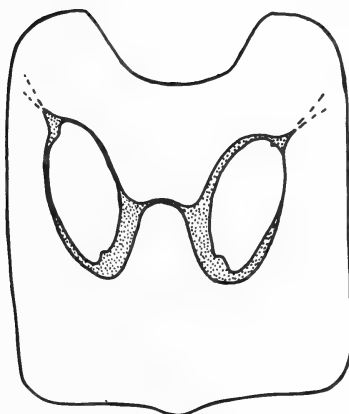
148



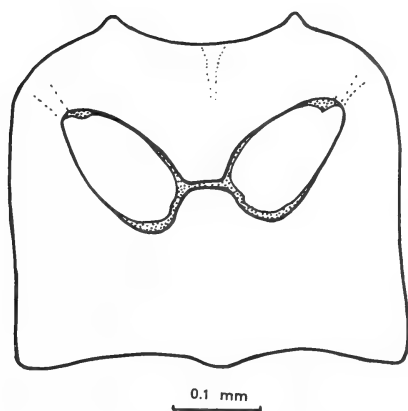
149



150



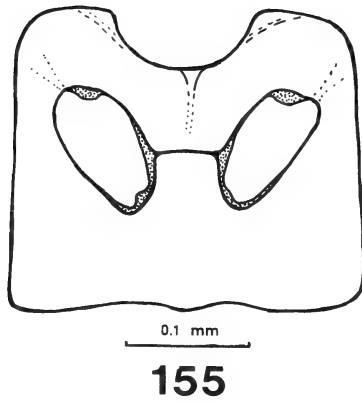
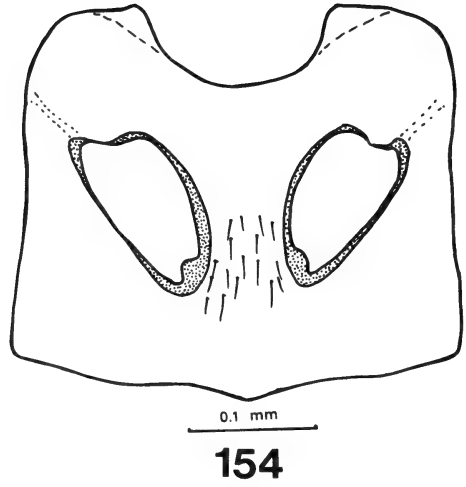
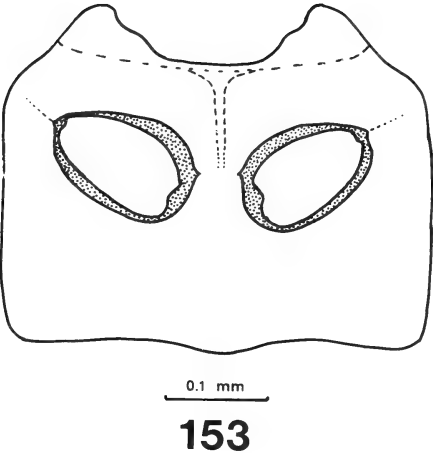
151



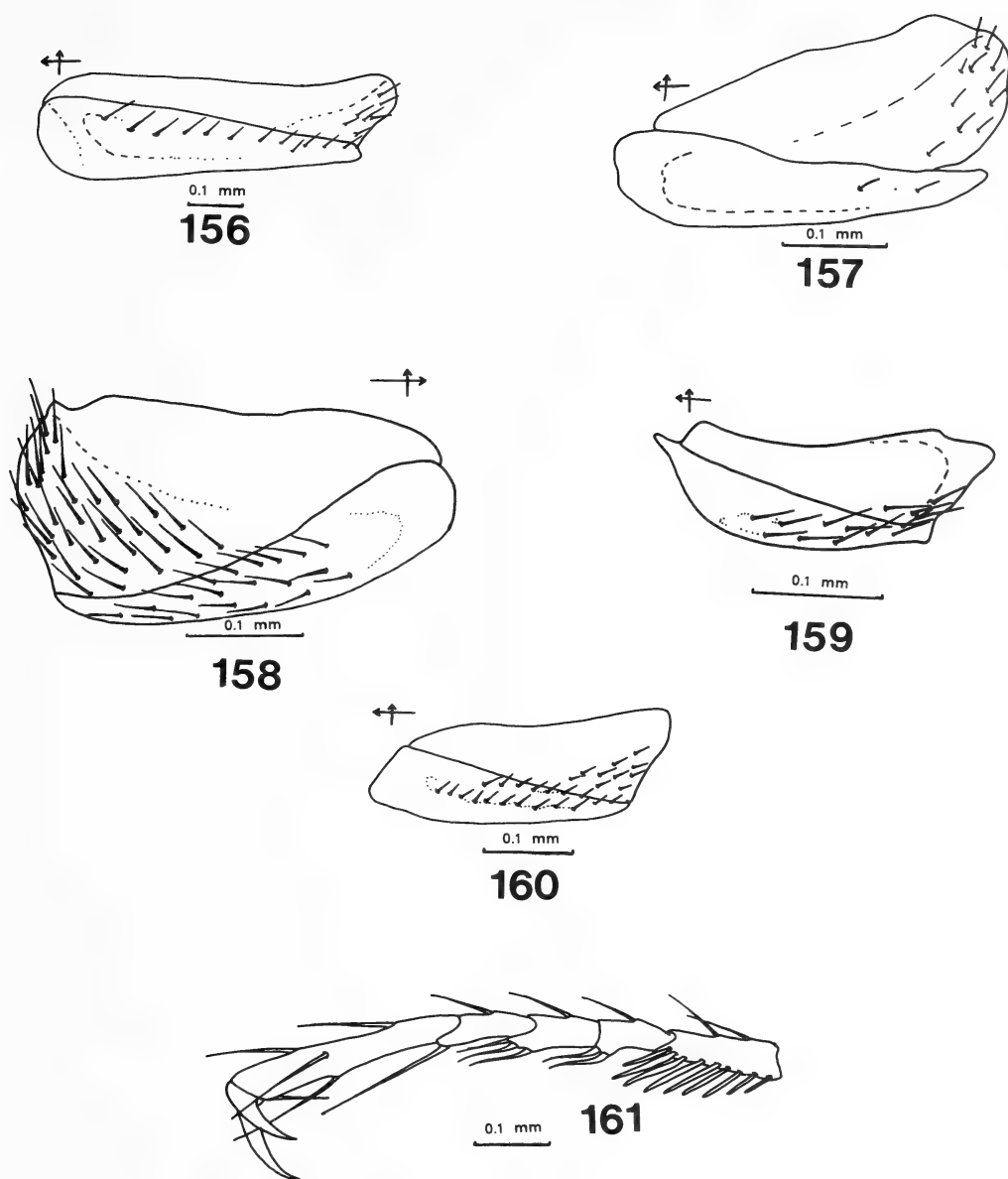
152

Figures 147-148. Illustrations of prosterna of adult Gyrophaenina. Fig. 147. *Sternotropa brevicornis* Cam. Fig. 148. *Agaricomorpha apacheana* (Seev.).

Figures 149-152. Illustrations of meso- and metasterna of adult Gyrophaenina. Fig. 149. *Gyrophaena nana* Payk. Fig. 150. *Gyrophaena blackwelderi* Seev. Fig. 151. *Phanerota fasciata* (Say). Fig. 152. *Agaricochara laevis* Kr.

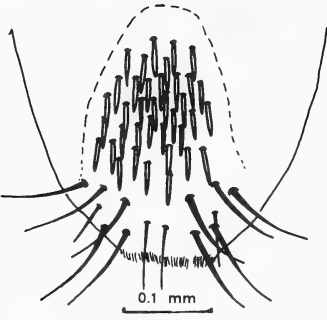


Figures 153-155. Illustrations of meso- and metasterna of adult Gyrophaenina. Fig. 153. *Sternotropa brevicornis* Cam. Fig. 154. *Pseudoligota varians* Cam. Fig. 155. *Agaricomorpha apacheana* (Seev.).

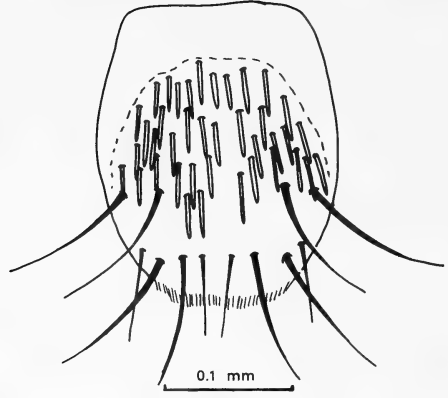


Figures 156-160. Illustrations of setal pattern on metepisternum and metepimeron of adult Gyrophaenina. (Small arrows indicate anterior and posterior directions.) Fig. 156. *Gyrophaena vitrina* Csy. Fig. 157. *Encephalus americanus* Seev. Fig. 158. *Brachida exigua* Heer. Fig. 159. *Pseudoligota varians* Cam. Fig. 160. *Agaricomorpha* undescr. sp.

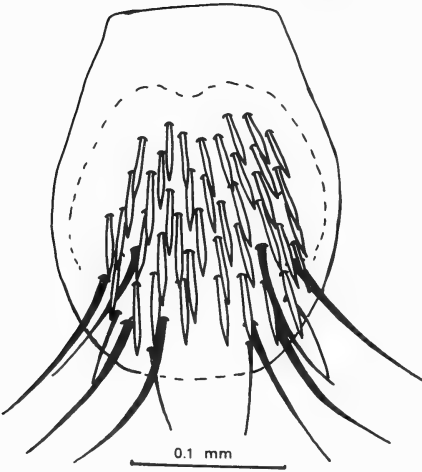
Figure 161. *Phanerota dissimilis* (Erichson), hind tarsus.



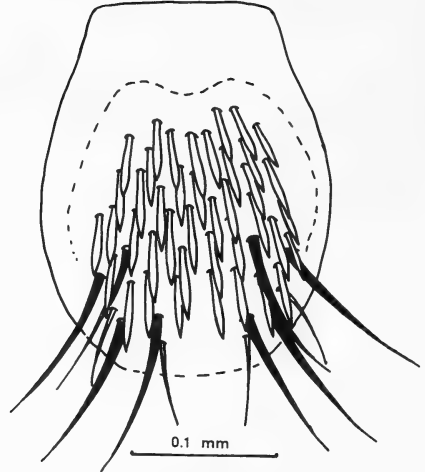
**162**



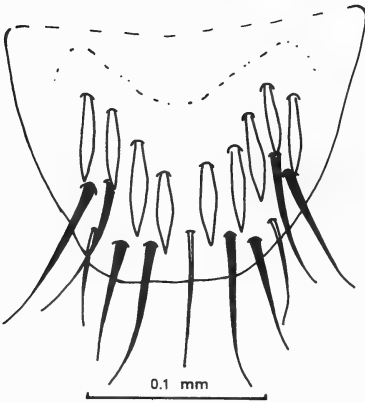
**163**



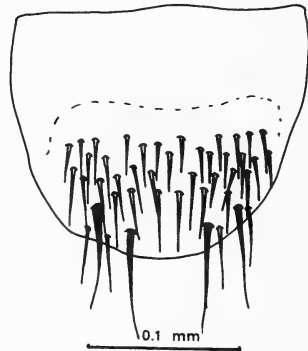
**164**



**165**

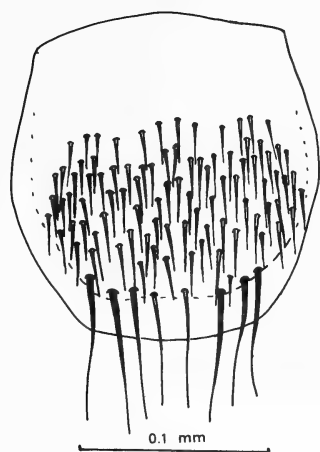
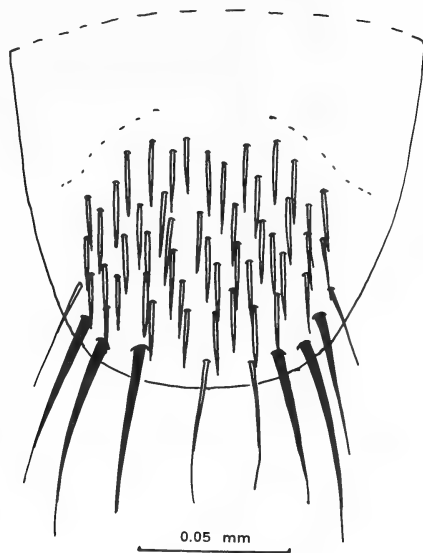
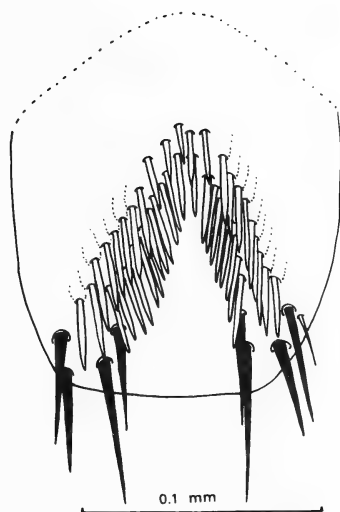
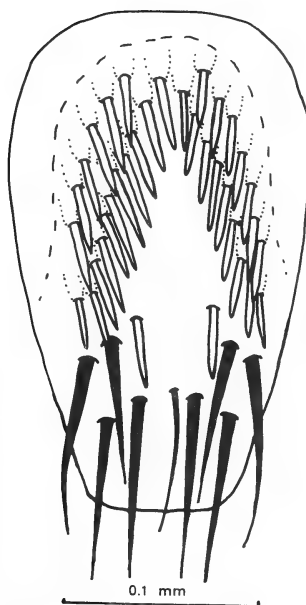


**166**

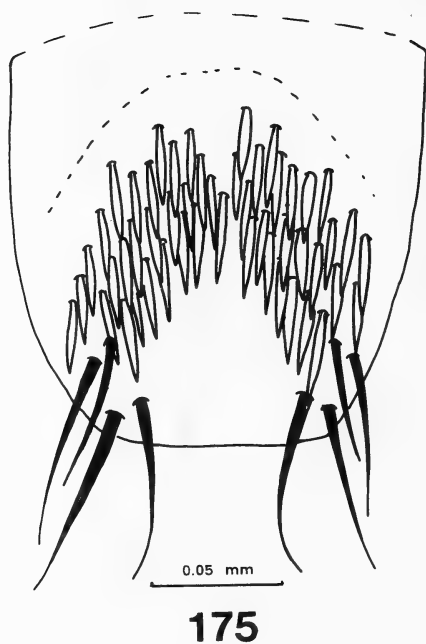
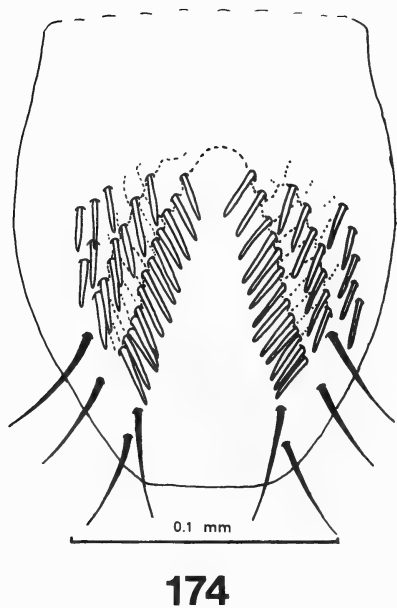
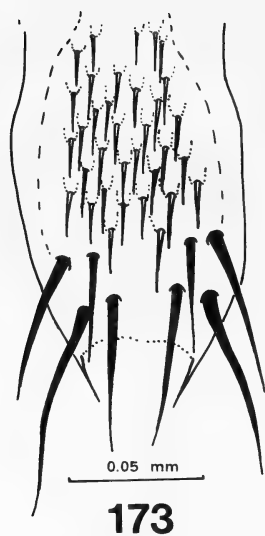
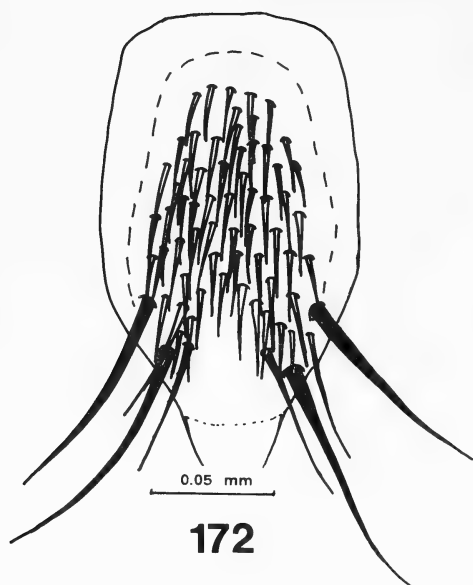


**167**

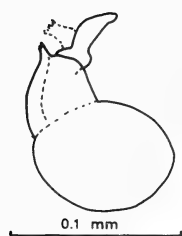
Figures 162-167 Illustrations of tergum 10 of adult Gyrophaenina. Fig. 162. *Gyrophaena antennalis* Csy. Fig. 163. *Gyrophaena blackwelderi* Seev. Fig. 164. *Phanerota fasciata* (Say). Fig. 165. *Phanerota dissimilis* (Erichson). Fig. 166. *Eumicrota corruscula* (Erichson). Fig. 167. *Encephalus zealandicus* Cameron.

**168****169****170****171**

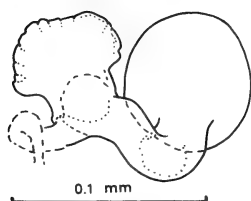
Figures 168-171 Illustrations of tergum 10 of adult Gyrophaenina. Fig. 168. *Probrachida geniculata* (Sharp). Fig. 169. *Agaricochara laeviscolis* Kr. Fig. 170. *Sternotropa brevicornis* Cam. Fig. 171. *Sternotropa flavicornis* Cam.



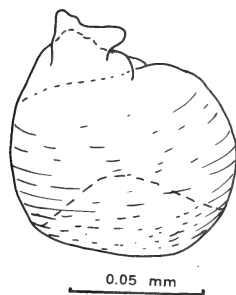
Figures 172-175 Illustrations of tergum 10 of adult Gyrophaenina. Fig. 172. *Pseudoligota varians* Cam. Fig. 173. *Pseudoligota affinis* Cam. Fig. 174. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 175. *Agaricomorpha apacheana* (Seev.).



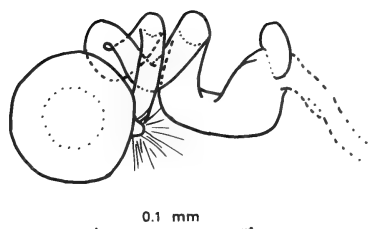
176



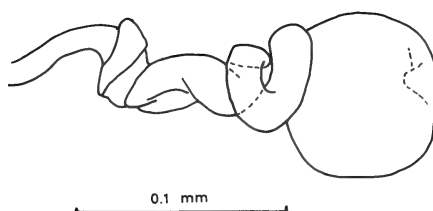
177



178



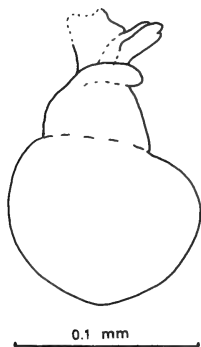
179



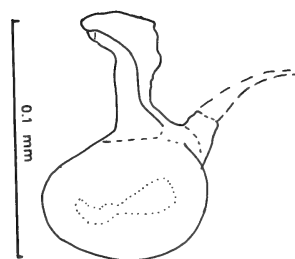
180



181

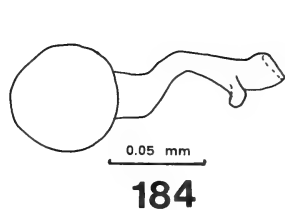


182

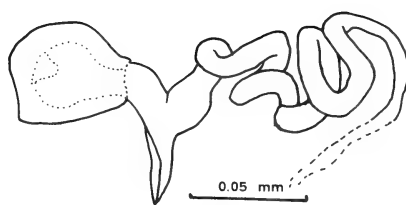


183

Figures 176-183. Illustrations of spermathecae of adult female Gyrophaenina. Fig. 176. *Gyrophaena nana* Payk. Fig. 177. *Gyrophaena blackwelderi* Seev. Fig. 178. *Gyrophaena frosti* Seev. Fig. 179. *Phanerota fasciata* (Say). Fig. 180. *Phanerota (Acanthophaena) insigniventris* (Cam.) Fig. 181. *Eumicrota corruscula* (Erichson). Fig. 182. *Encephalus complicans* Kirby. Fig. 183. *Encephalus zealandicus* Cameron.



184



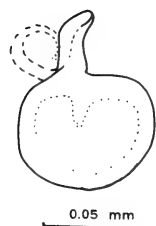
185



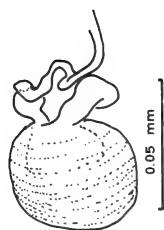
186



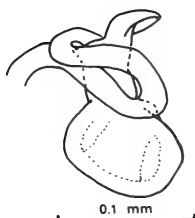
187



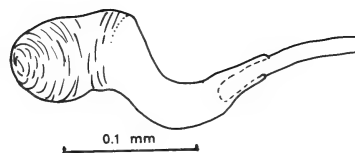
188



189



190

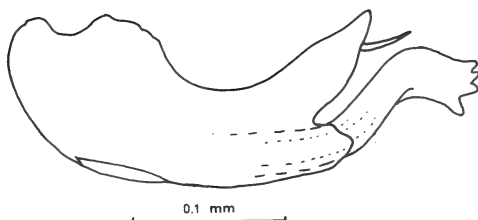
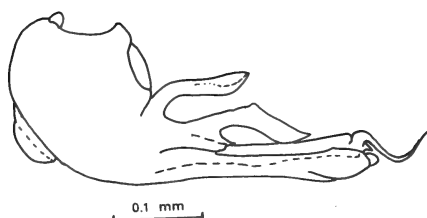
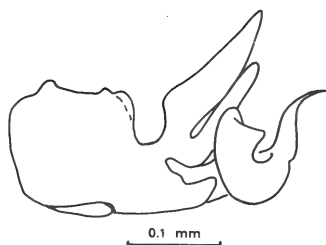
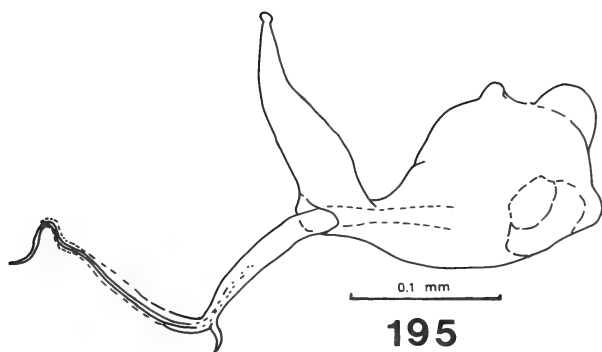
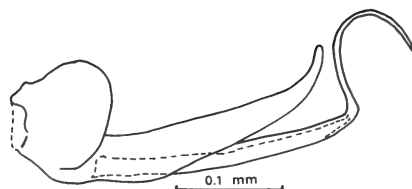


191

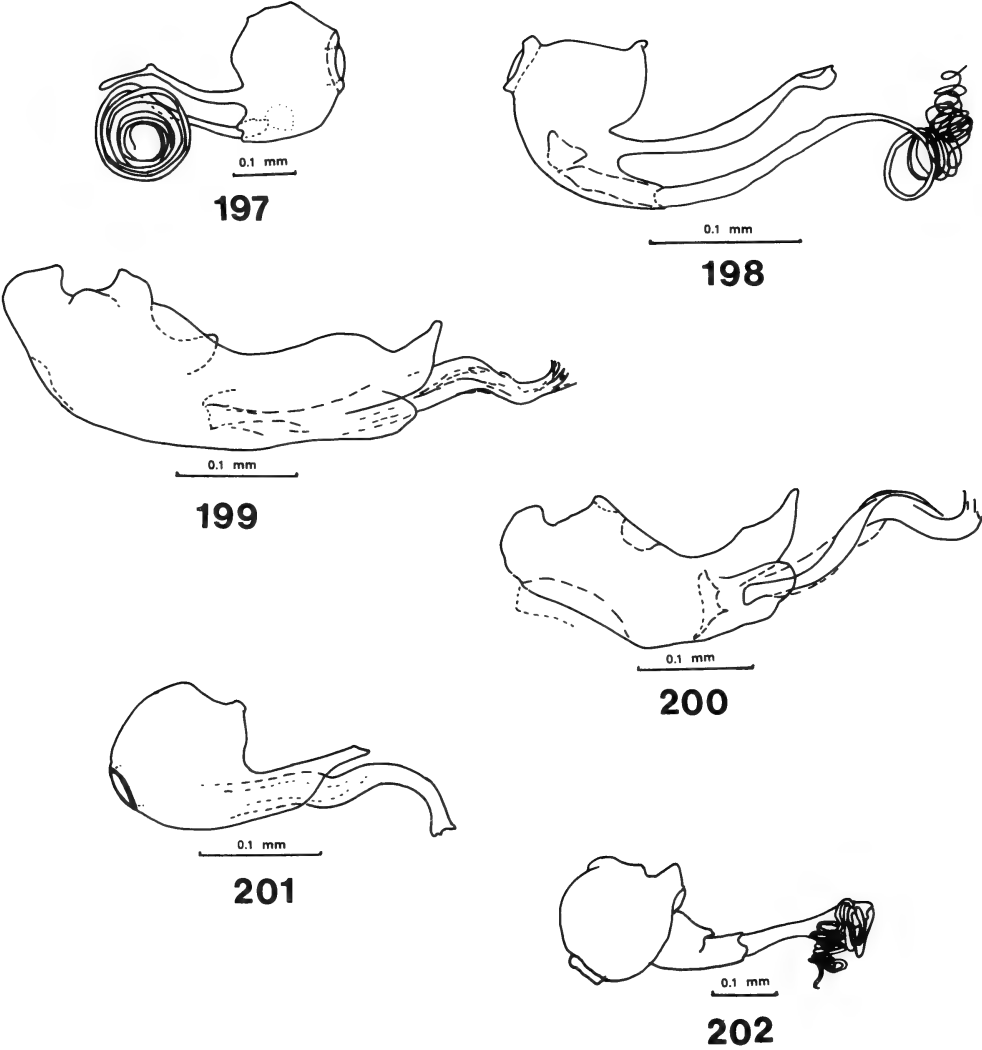
Figures 184-190. Illustrations of spermathecae of adult female Gyrophaenina. Fig. 184. *Probrachida* undescr. sp. Fig. 185. *Brachida exigua* Heer. Fig. 186. *Agaricochara laeviscollis* Kr. Fig. 187. *Sternotropa brevicornis* Cam. Fig. 188. *Pseudoligota varians* Cam. Fig. 189. *Brachychara* sp. (prob. *B. crassa* Sharp). Fig. 190. *Agaricomorpha apacheana* (Seev.).

Figure 191. *Bolitochara lunulata* Gyll., spermatheca.

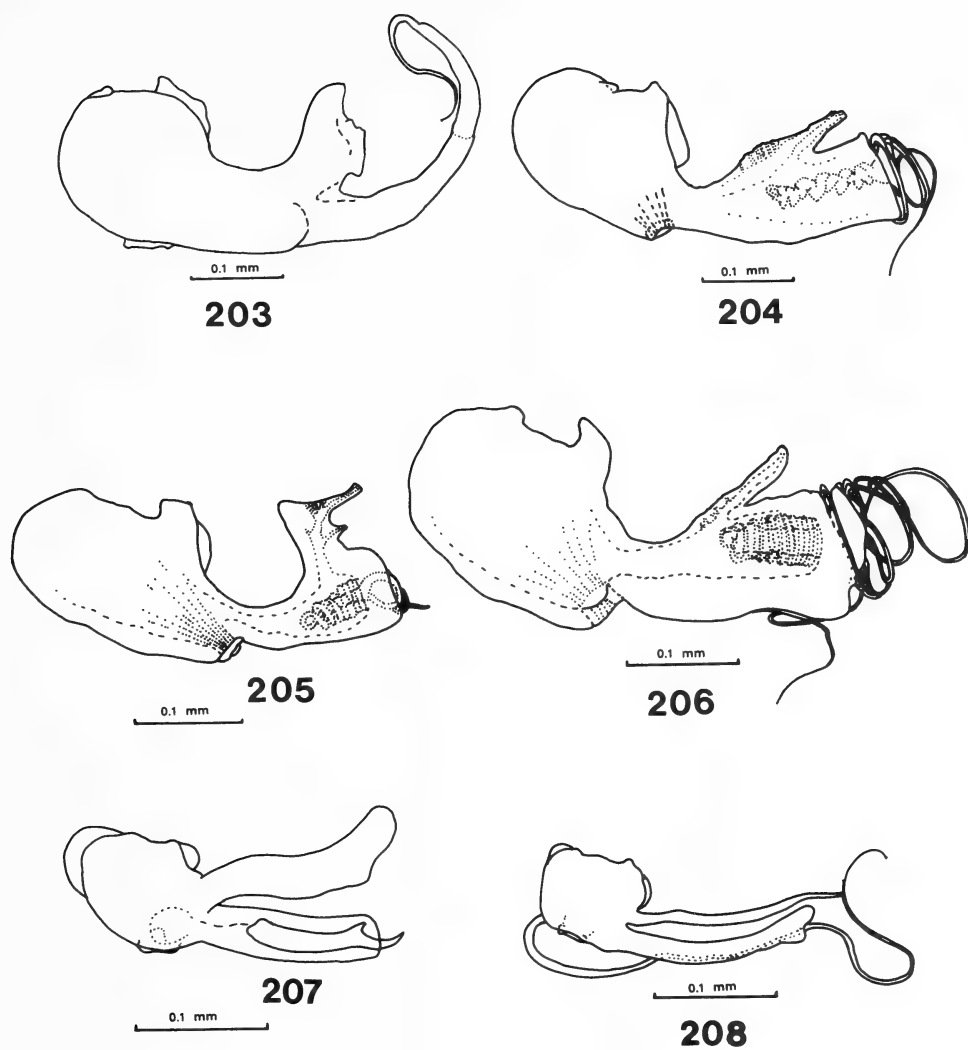


**192****193****194****195****196**

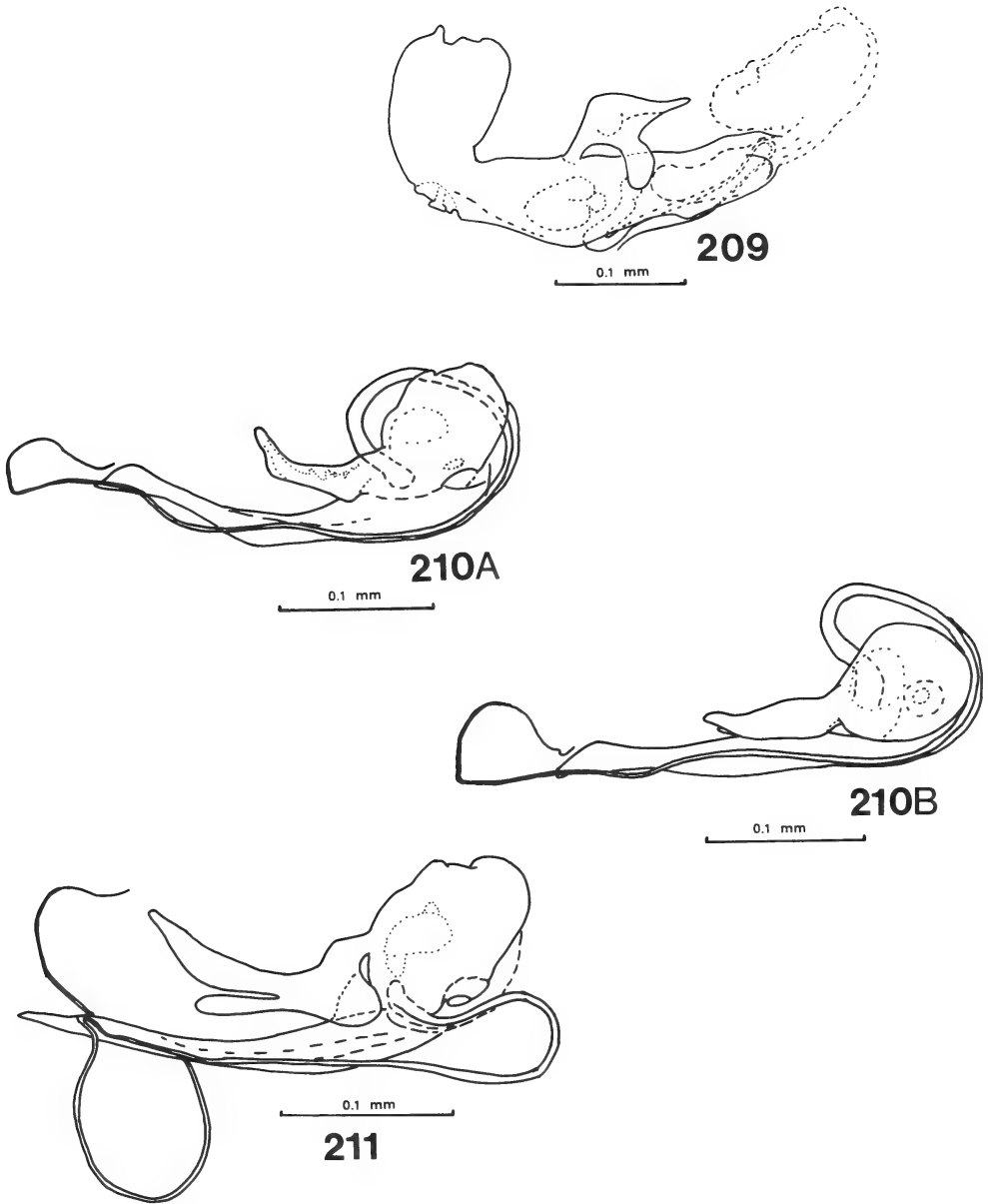
Figures 192-196. Illustrations of median lobe of aedeagus of adult male Gyrophaenina. Fig. 192. *Gyrophaena nana* Payk. Fig. 193. *Gyrophaena antennalis* Csy. Fig. 194. *Gyrophaena affinis* Sahlb. Fig. 195. *Phanerota dissimilis* (Erichson). Fig. 196. *Phanerota* (*Acanthophaena*) *insigniventris* (Cam.)



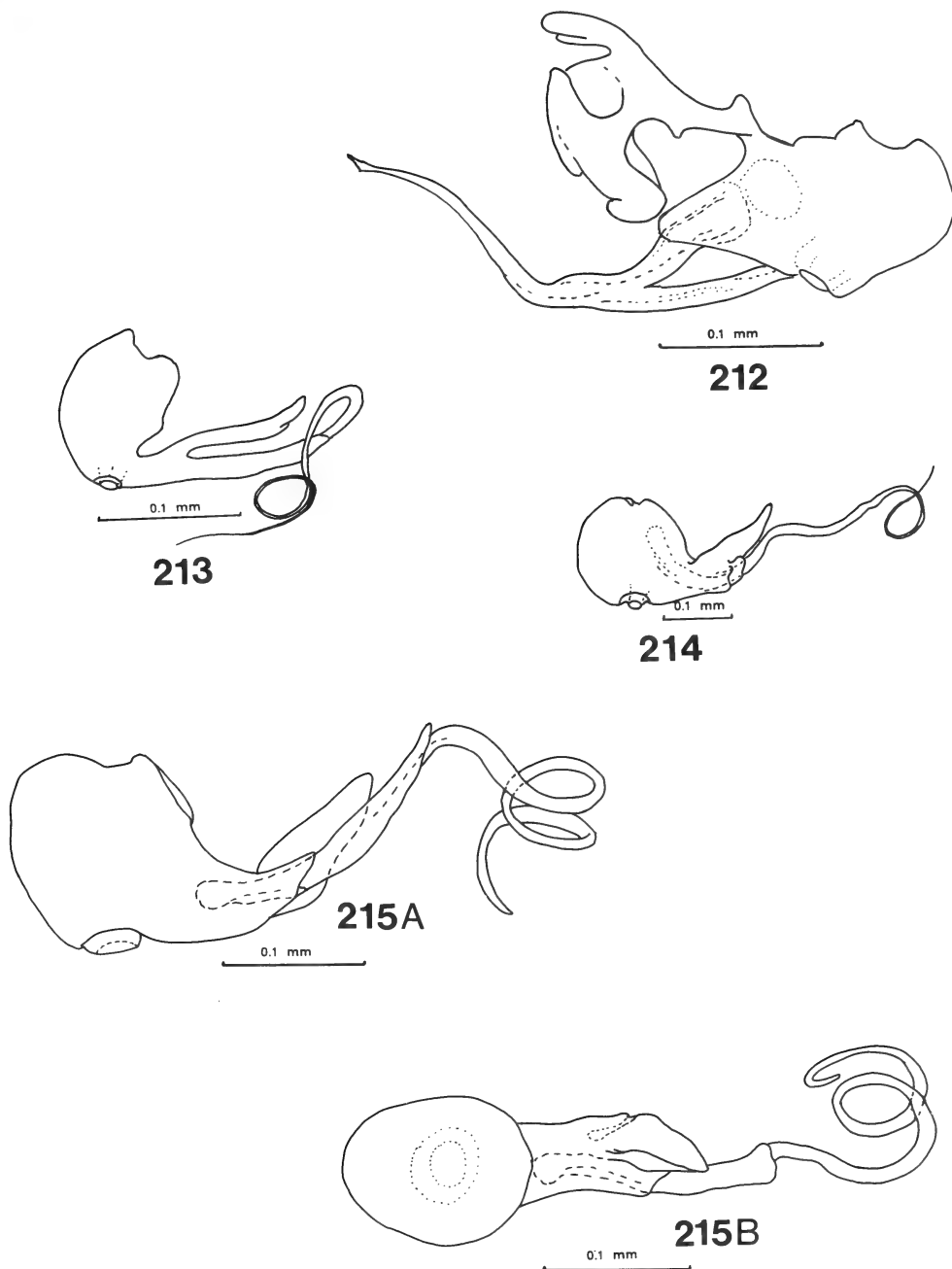
Figures 197-202. Illustrations of median lobe of aedeagus of adult male Gyrophaenina. Fig. 197. *Eumicrota corruscula* (Erichson). Fig. 198. *Eumicrota undescr.* sp. Fig. 199. *Encephalus complicans* Kirby. Fig. 200. *Encephalus americanus* Seev. Fig. 201. *Encephalus zealandicus* Cameron. Fig. 202. *Probrachida modesta* (Sharp).



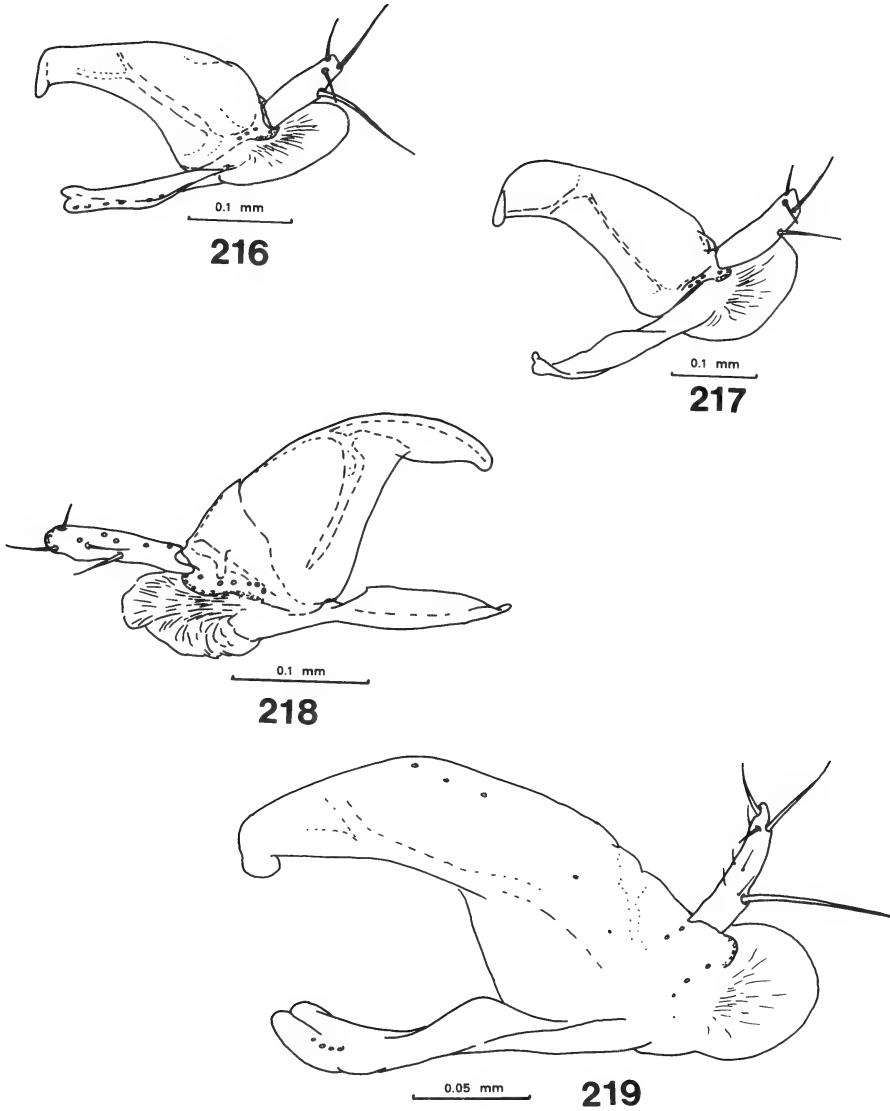
Figures 203-208. Illustrations of median lobe of aedeagus of adult male Gyrophaenina. Fig. 203. *Probrachida reyi* (Sharp). Fig. 204. *Brachida exigua* Heer. Fig. 205. *Brachida africana* Bernh. Fig. 206. *Brachida sublaevipennis* Cam. Fig. 207. *Agaricochara laevicollis* Kr. Fig. 208. *Sternotropa nigra* Cam.



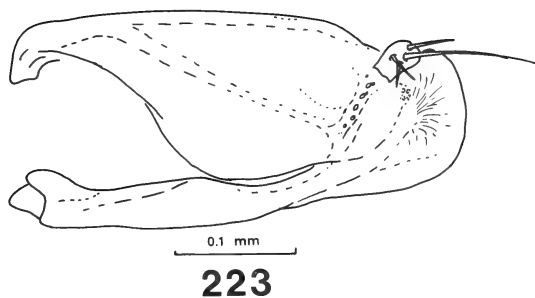
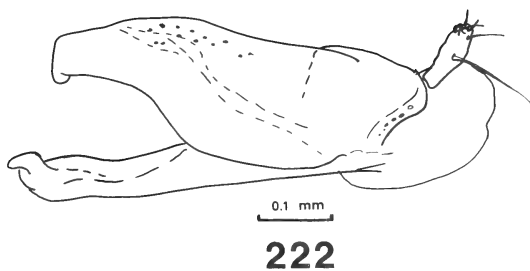
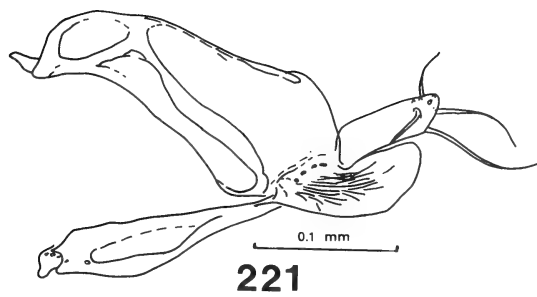
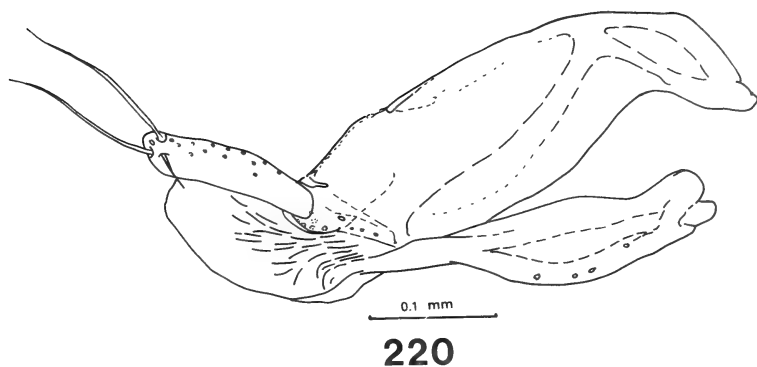
Figures 209-211. Illustrations of median lobe of aedeagus of adult male Gyrophaenina. Fig. 209. *Sternotropa elevata* (Fvl.). Fig. 210. *Pseudoligota varians* Cam., A) lateral aspect, B) dorsal aspect. Fig. 211. *Pseudoligota affinis* Cam.



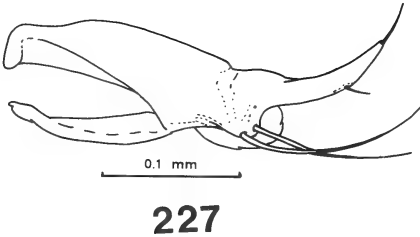
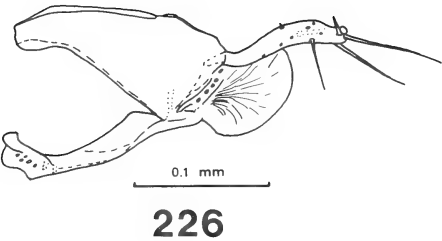
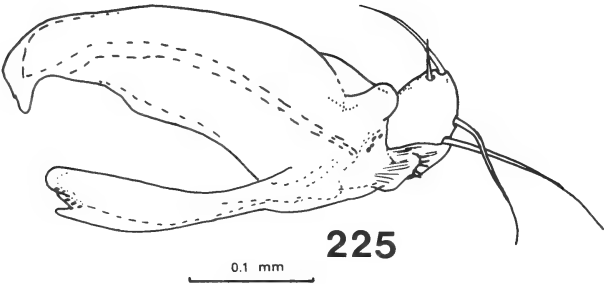
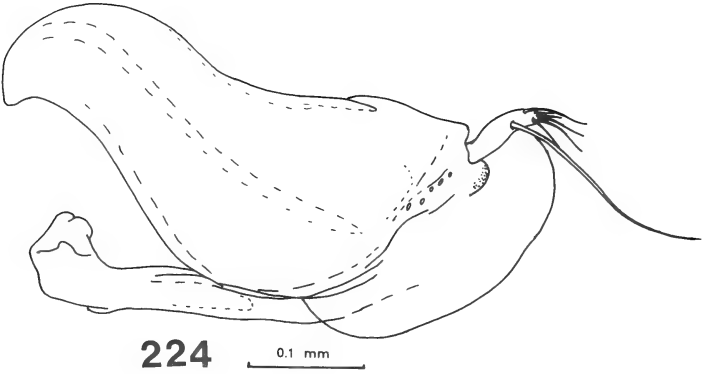
Figures 212-215. Illustrations of median lobe of aedeagus of adult male Gyrophaenina. Fig. 212. *Adelarthra barbari* Cam. Fig. 213. *Brachychara brevicornis* Sharp. Fig. 214. *Agaricomorpha apacheana* (Seev.). Fig. 215. *Agaricomorpha* undescr. sp., A) lateral aspect, B) dorsal aspect.



Figures 216-219. Illustrations of parameres of aedeagi of adult male Gyrophaenina. Fig. 216. *Gyrophaena nana* Payk. Fig. 217. *Gyrophaena frosti* Seev. Fig. 218. *Phanerota dissimilis* (Erichson). Fig. 219. *Eumicrota corruscula* (Erichson).

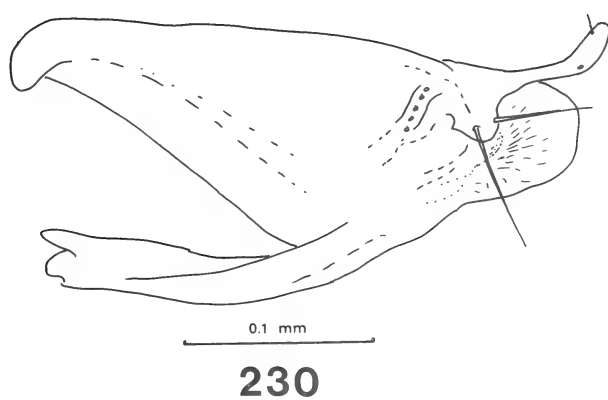
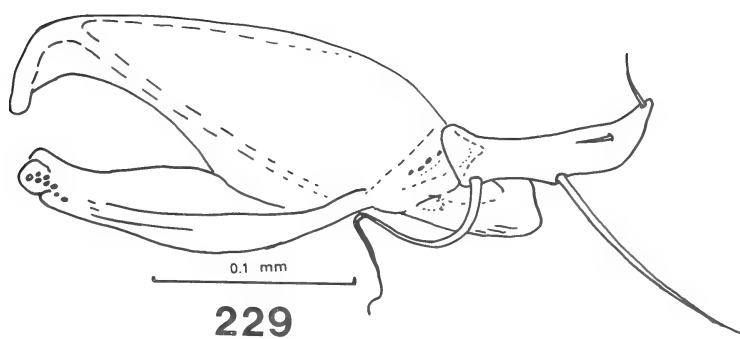
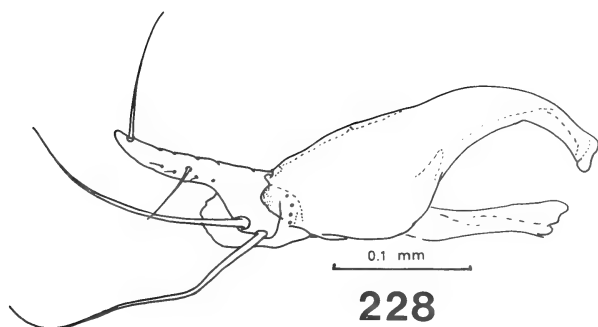


Figures 220-223. Illustrations of parameres of aedeagi of adult male Gyrophaenina. Fig. 220. *Encephalus complicans* Kirby. Fig. 221. *Encephalus americanus* Seev. Fig. 222. *Probrachida modesta* (Sharp). Fig. 223. *Probrachida reyi* (Sharp).



Figures 224-227. Illustrations of parameres of aedeagi of adult male Gyrophaenina. Fig. 224. *Probrachida sparsa* (Sharp). Fig. 225. *Brachida exigua* Heer. Fig. 226. *Agaricochara laevicollis* Kr. Fig. 227. *Sternotropa nigra* Cam.





Figures 228-230. Illustrations of parameres of aedeagi of adult male Gyrophaenina. Fig. 228. *Sternotropa elevata* (Fvl.). Fig. 229. *Pseudoligota affinis* Cam. Fig. 230. *Adelarthra barbari* Cam.

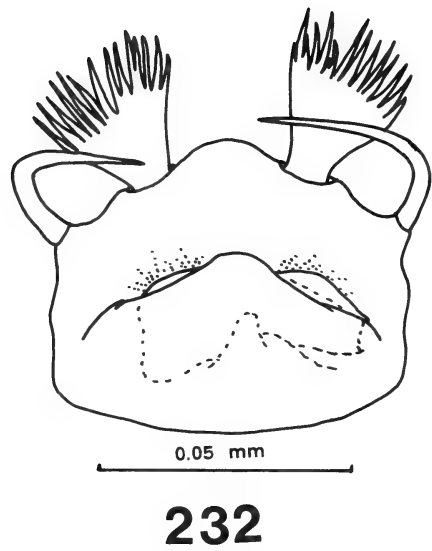
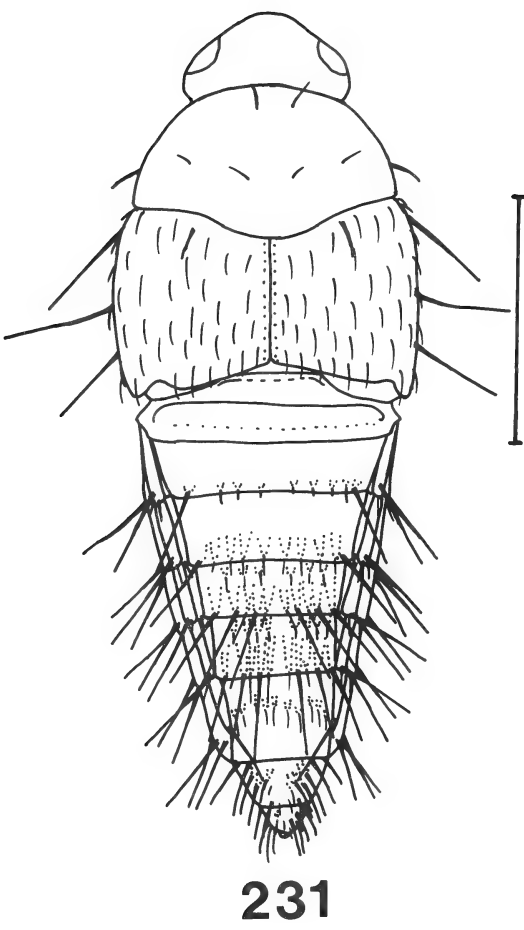
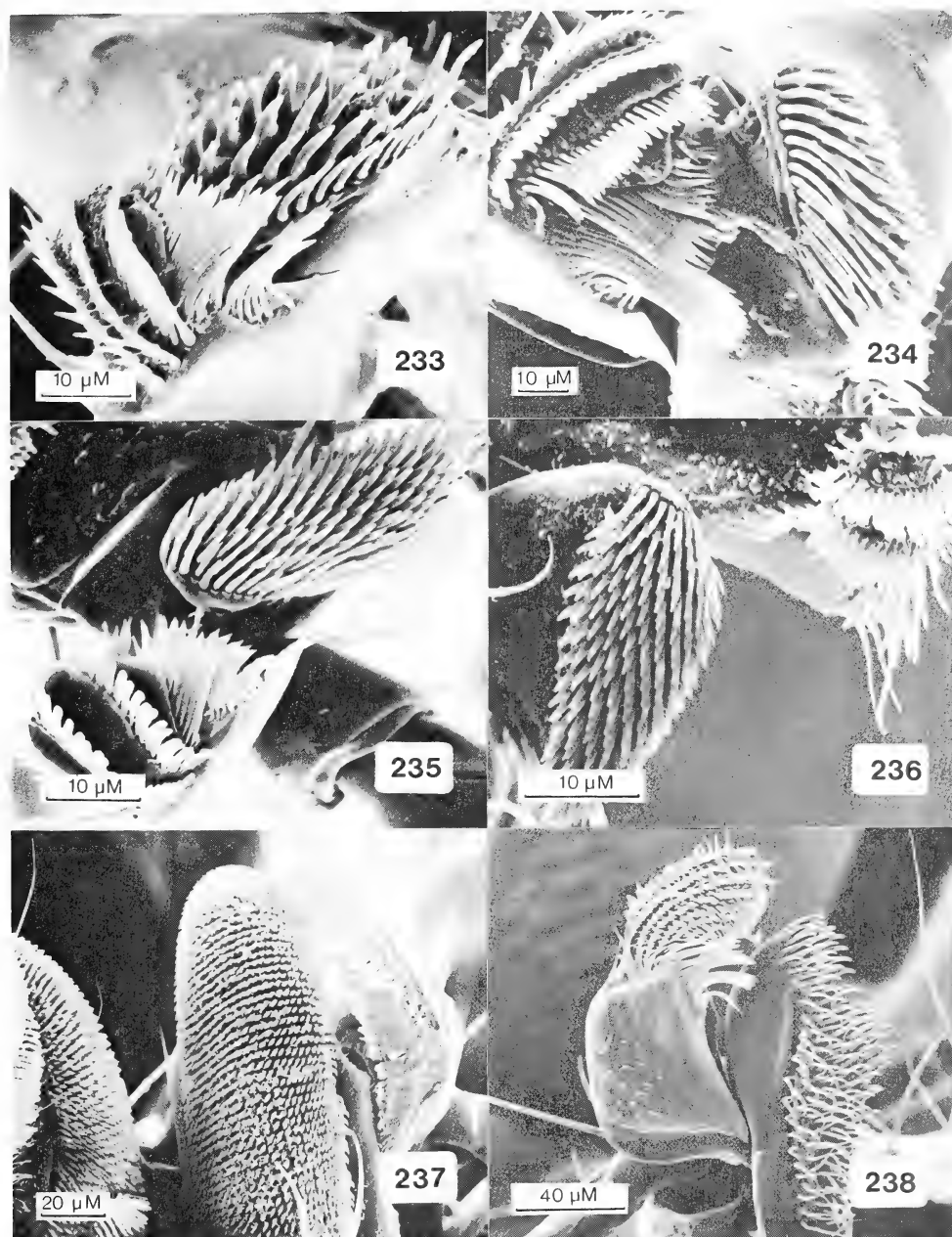


Figure 231. *Adelarthra barbari* Cam., dorsal aspect of body. (Scale line = 0.3mm).

Figure 232. *Brachychara* sp.; larva, instar 3; apical aspect of tergum 8 showing brush-like setae.



Figures 233-238. SEM micrographs of maxillae of adult Gyrophaenina and Bolitocharina. Fig. 233. *Gyrophaena nana* Payk., right maxilla, apex of galea and lacinia. Fig. 234. *Gyrophaena gilvicollis* Csy., right maxilla, apex of galea and lacinia. Fig. 235. *Eumicrota corruscula* (Erichson), right maxilla, apex of galea and lacinia. Fig. 236. *Agaricomorpha apacheana* (Seev.), left maxilla, apex of galea and lacinia. Fig. 237. *Brachychara* sp. (prob. *B. crassa* Sharp), maxillae, apex of galea and lacinia. Fig. 238. *Bolitochara lunulata* Gyll., left maxilla, apex of galea and lacinia.

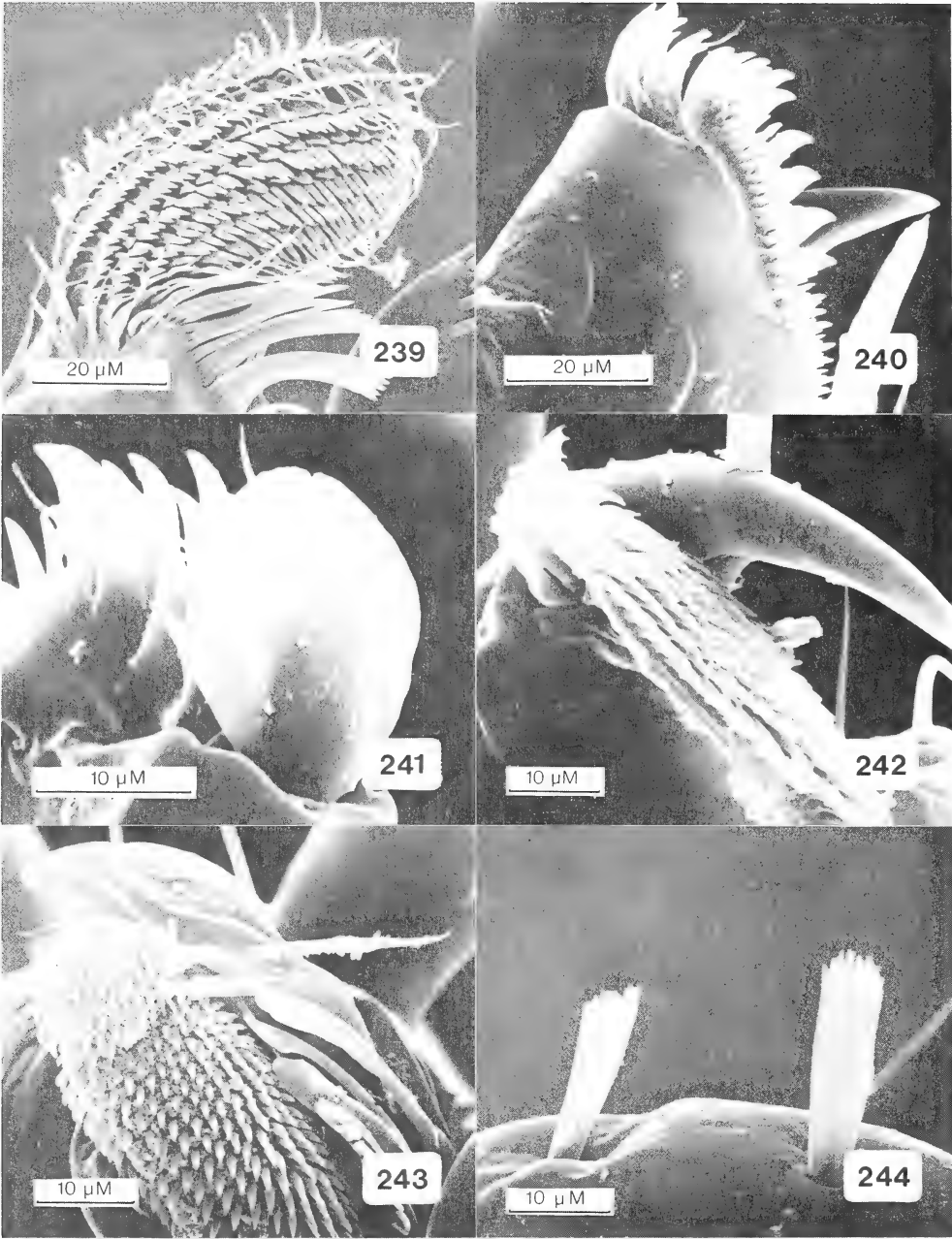
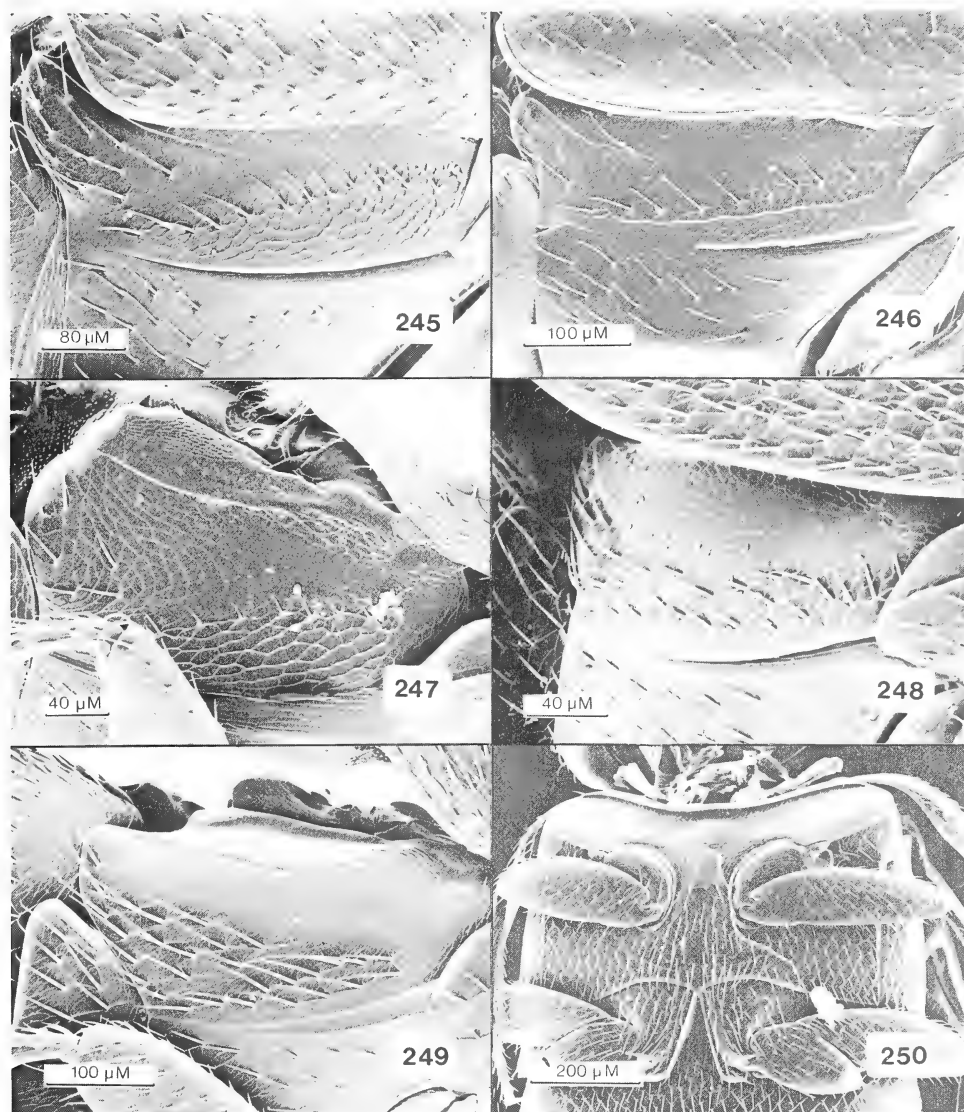


Figure 239. *Bolitochara lunulata* Payk., adult, apex of galea. SEM micrograph.

Figures 240-244. SEM micrographs of structures of larval (instar 3) Gyrophaenina. Fig. 240. *Gyrophaena nana* Payk., maxilla, apex of mala. Fig. 241. *Gyrophaena nana* Payk., maxilla, outer apical aspect of mala showing leaf-like scale. Fig. 242. *Agaricomorpha apacheana* (Seev.), left maxilla, apex of mala. Fig. 243. *Brachychara* sp. (prob. *B. crassa* Sharp), right maxilla, apex of mala. Fig. 244. *Agaricomorpha apacheana* (Seev.), apical aspect of tergum 8 showing brush-like seta.



Figures 245-249. SEM micrographs of metepisterna and metepimera of adult Gyrophaenina. Fig. 245. *Gyrophaena nana* Payk. Fig. 246. *Gyrophaena gilvicollis* Csy. Fig. 247. *Eumicrota corruscula* (Erichson). Fig. 248. *Agaricomorpha apacheana* (Seev.). Fig. 249. *Brachychara* sp. (prob. *B. crassa* Sharp).

Figure 250. *Brachychara* sp. (prob. *B. crassa* Sharp), adult, ventral aspect, mesosternum and metasternum.

## NATURAL HISTORY OF GYROPHAENINA

**Habitat**

*General Distribution.*— As far as is known, all gyrophaenines are obligatory inhabitants of fresh fruiting bodies of gilled and polypore mushrooms as both larvae and adults. However, as discussed more fully later (see Evolutionary Trends), gyrophaenines are seldom encountered on many groups of fungi producing fruiting bodies commonly called “mushrooms”. Adults colonize mushrooms soon after spore producing tissue is exposed, and both larvae and adults are found on more mature mushrooms. Both adults and larvae feed exclusively by “grazing” on the spore producing layer (the hymenium). Because of this requirement for an active hymenium layer, gyrophaenines inhabit only fresh mushrooms. By the time the mushroom begins to decay all gyrophaenines (both larvae and adults) have usually left.

Adults and larvae of those gyrophaenines which live on gilled mushrooms are in spaces between the gills. They are almost never on the cap, stem, base or other parts of the mushroom, and they do not burrow into the flesh of the mushroom.

Adults and larvae of those species which normally live on polypore mushrooms are usually found on the pore surface. Pores of many polypores are too small to admit the beetles. However, some polypores have larger pores (*e.g. Daedalea* and related species), and both larvae and adults are commonly found in the pore tubes or sinuations.

Because of the apparent affinity of gyrophaenines for tight places, both larvae and adults of those species on polypores often take refuge from the exposed pore surface in cracks, crevices, holes due to insect damage, and under bits of bark at the base of the mushroom.

Occasionally adults and very rarely larvae are found under or in logs, especially if fungus covered, or in leaf litter at the base of logs. Adults may also be found in moist or moldy leaf litter or in leaf litter beneath mushrooms.

Specimens of some genera (*Brachida*, *Encephalus*) are not commonly found on mushrooms. Little is known about habits of members of these genera. *Brachida exigua* (Heer) is collected in Europe most commonly from grass tufts and ground litter (Lohse, 1974), but Benick (1952) reports it from a tree-fungus. *Encephalus complicans* Kirby is commonly collected in hay and rotting grass, often in bogs (Lohse, 1974).

No habitat information is available for specimens of *Probrachida*. I have collected two specimens at light, and I have seen one specimen from “moist litter”. Unfortunately, Sharp (1883–1887) did not provide collecting data for members of this genus.

Cameron (1939) reported *Adelarthra barbari* from “rotten log” and “in log with ants”. Label data from the two known specimens of this species are “debris” and “wood (rotten)”. These may have been associated with fungus (probably polypores) on the logs. An obligatory or facultative association with ants seems unlikely.

Gyrophaenines are rarely found on rotting fruit or by sweeping vegetation. These are almost certainly atypical habitats for these insects.

*Aggregation of gyrophaenines.*— Adults, and, on more mature mushrooms, larvae, are commonly found in very large numbers on mushrooms. For example, in one collection more than 750 individual adult gyrophaenines were collected from a single fruiting body of *Amanita verna* (Fr.) Quel. While this large number of individuals per mushroom is exceptional, it is common to find tens of individuals per mushroom, and not unusual to find 100 or more individuals per mushroom.

Fenyés (1918–21) (after Ganglbauer) stated that specimens of *Gyrophaena* form “colonies” on gilled mushrooms. This may be taken to imply some sort of societal organization and is

misleading. Gyrophaenines are opportunists and are simply attracted individually to fresh mushrooms where they form aggregations.

There is, however, some evidence that gyrophaenines may be gregarious. In many groups of mushrooms of the same species, one or a few of the fruiting bodies have large concentrations of gyrophaenines, while others have few or none of these beetles on them. In addition, on a single collecting trip many fruiting bodies of a species of mushroom may be sampled which produce few or no gyrophaenines, then a specimen will be found on which gyrophaenines are concentrated in large numbers. This suggests that gyrophaenines may be actively aggregating. A possible aggregation mechanism might be use of pheromones. Such aggregation pheromones have been hypothesized for fungus beetles of the family Ciidae (Lawrence, 1973).

Advantages of aggregation might include increased contact and subsequently better mating success, and perhaps certainty of being attracted to a mushroom already found to be a suitable host by other gyrophaenines. There are, however, other possible explanations (other than active aggregation) for these discontinuous distributions. These include undetected differences in age or physiological condition of the mushroom and possibly chance (random) effects such as a fruiting body developing near a previous concentration of gyrophaenines (e.g., a concentration of larvae which emerge to adults, overwinter concentration, concentration of adults leaving a nearby previously occupied mushroom, etc.).

*Feeding Habits.*— All gyrophaenines appear to be totally mycophagous as both larvae and adults. There is no indication that they are predaceous (even facultatively) at any stage of the life cycle. Both larvae and adults “graze” maturing spores, basidia, cystidia and hyphae from the hymenium layer of the mushroom. White (1977: 307) reports that feeding activities of gyrophaenines leave “broad lines over the gill surface where spores and basidia are absent”. My own observations concur.

Maxillae of gyrophaenines appear to be the main feeding structures. They are strikingly modified for “grazing” on the hymenium layer of mushrooms (see Adaptations to the Mushroom Habitat), rapidly scraping the hymenium as the beetle feeds. The mandibles usually also work at the same time as the maxillae. However, grazing movements by the maxillae are often observed without corresponding movements of the mandibles.

Function of the mandibles is unclear. They are not highly modified for fungus feeding. They could serve as a shearing device, but this seems unlikely since they are above the maxillae in relation to the hymenial surface. They may also scrape the collected fungus material from the spore brush of the maxillae and form it into a bolus. Seevers (1978) noted that all bolitocharines have a molar region on the inner face of the mandibles beset with rows of small denticles. He suggested that this is an adaptation for eating hyphae and spores of fungi. All Gyrophaenina have well developed rows of small teeth on the molar region. This region of the mandible possibly grinds spores and hyphae grazed from the hymenium. However, whole mount slide preparations of many species of gyrophaenines indicate that in normal position, the molar surfaces of the mandibles are quite distant from each other, and probably cannot grind against one another. It remains possible that these surfaces grind food against ridges on the epipharynx. In this regard, it is interesting to note that while the maxillae of gyrophaenine larvae are remarkably like those of adults, the mandibles are much simpler and lack a molar surface. Therefore, although larvae appear to be scraping the hymenium in a way similar to that of adults, they apparently do not have to subsequently grind the material thus obtained.

Those gyrophaenines which live exclusively on polypore fungi often cannot get into the pores of the mushroom to feed directly on the hymenial layer. Therefore, they may have a

fundamentally different feeding activity than the hymenium “grazing” of those gyrophaenines which live on gilled mushrooms, or those which live on polypores with large pores. I have not observed feeding activity of gyrophaenines on polypores with very small pores, nor has this been described in the literature. It seems likely that larvae and adults of these beetles simply graze the maturing spores, hyphae and basidia which protrude from the pore mouths. This is suggested by examination of gut contents of larvae of *Agaricomorpha apacheana* (SeEVERS). Larvae and adults of this species live in *Fomes* species in the southwestern U.S. Fruiting bodies of this fungus have very tiny pores. Guts of these larvae were filled with a mixture of mature fungus spores, broken cells, and masses of hyphae. Interestingly, those gyrophaenines which live on woody polypore mushrooms have a lacinial spore brush with relatively more numerous, closely spaced, shorter teeth (in comparison to those which live on gilled mushrooms). This spore brush structure is probably in some way related to requirements of feeding on woody polypores (see Adaptations to the Mushroom Habitat).

### Life History

*Diel Activity Patterns.*— Very little is known about the daily activity patterns of gyrophaenines, and virtually nothing has been published on this aspect of gyrophaenine natural history. However, some circumstantial evidence seems to indicate that gyrophaenines are mostly diurnal.

Ashe (1981a) reports colonization of mushrooms by adults of *Phanerota fasciata* (Say) late in the afternoon. In addition, I have observed instances of colonization of mushrooms by various species of *Gyrophaena*. All were during the day and most were mid- to late afternoon. These observations, though, may only reflect a temporal collecting bias.

All gyrophaenine species have well developed eyes (particularly large in *Phanerota* species). This suggests that vision plays a role in orientation to, or colonization of, mushrooms. While it is true that a few gyrophaenines are found at lights, they are not abundant there, and certainly gyrophaenines do not form part of the typical assemblage of staphylinids found at lights. This suggests that gyrophaenines do not have major periods of dispersal at dusk or during evening, characteristic of many staphylinids — in particular those which live in many other temporary habitats.

Feeding by larvae and both mating and feeding by adult gyrophaenines have been observed numerous times on mushrooms during daylight hours. I do not know if these activities continue during periods of darkness. However, rapid growth of gyrophaenine larvae, especially the very short duration of instars I and II (see below), suggests that feeding may be almost constant, at least during early stages. Continuous feeding activity may be a requirement of those species which live on rapidly decaying gilled mushrooms. Nothing is known of activity patterns of those gyrophaenines which live on more persistent polypore mushrooms. However, the requirement for rapid larval development may be less stringent in these habitats, and this may in turn affect the diel activity patterns of larvae of those species which occur there.

In addition, several instances in which ecdysis from instar I to II or instar II to III occurred during periods of darkness are known (personal observations) further suggesting that activity may be continuous.

In summary, although there is little direct observation of daily activity of gyrophaenines, circumstantial evidence suggests the following may be characteristic. Adults are predominately diurnal, and dispersal and colonization of fresh mushrooms occurs during the day. However, sporadic adult activity may occur at night. Larval activity may be virtually continuous



throughout a 24 hour period, but this may vary according to the specific mushroom habitat used.

*Life Cycle and Seasonal Activity.*— In comparison to the marked diversity of gyrophaenines little detailed information about life history and seasonal activity is available. Much must be inferred from circumstantial evidence. The only detailed study of life history of a gyrophaenine was about *Phanerota fasciata* (Say) (Ashe, 1981a). Because of this study, natural history of those species which live on gilled mushrooms is better known. Great opportunity exists for life history studies within the gyrophaenines. Ashe (1981a) emphasized the ease with which these may be done.

Because adults mate, lay eggs and feed, and larvae mature on a mushroom before it rots, ability to find and colonize young fresh fruiting bodies is of vital importance to gyrophaenines. Adult gyrophaenines are often among the first insects to colonize fresh mushrooms, and are often found in gilled mushrooms soon after the gills are exposed. Colonization apparently occurs by adults flying to the fresh mushrooms. Ashe (1981a) reports adults of *Phanerota fasciata* flew over the mushroom, landed on the cap, then ran around to the undersides. I have observed similar activity by members of other species.

It is not known how gyrophaenines find mushrooms. However, mushrooms produce a variety of volatile chemicals, and it is reasonable to expect that at least part of the attraction of gyrophaenines to mushrooms is an olfactory response to these chemicals.

Gyrophaenines may make the decision about whether a mushroom is a suitable host before or after arriving on the mushroom. Adults may respond only to mushrooms with certain chemical and physical characteristics. On the other hand, gyrophaenines may be attracted to a wide variety of mushrooms and accept or reject each as a host after exploratory feeding or other activities on the mushroom. It is most likely that both of these are factors in host choice.

Although the mechanism of host finding by gyrophaenines is unknown, it is, as indicated above, apparently quite efficient.

I have observed mating by gyrophaenines including *P. fasciata* (Ashe, 1981a) on both polypores and gilled mushrooms, and surmise that mating normally occurs on the mushroom.

Mating by members of *P. fasciata* is similar to that described for *Aleochara curtula* by Peschke (1978). The male bends the abdomen forward over his dorsum, extrudes the aedeagus and attempts to make contact with the female's abdomen. If contact is effected, the median lobe of the aedeagus is inserted into the genital chamber of the female and copulation is initiated. Among most aleocharines which use this mating position male and female may face in the same direction with the male slightly behind and to one side of the female. This orientation is commonly found among gyrophaenines. However, among those which occur in gilled mushrooms, a slightly different mating configuration is often observed. After copulation is initiated as described above, the male may straighten his abdomen and take a position on the mushroom gill facing the one the female is on. In this position the bodies of the male and female form an angle of 180° to each other, face in opposite directions, and each is upside down in relation to the other. This position has been described in *P. fasciata* (Ashe, 1981a) and I observed it in a number of species of *Gyrophaena* which live in gilled mushrooms.

This position is a relatively simple modification of the "typical" mating orientation and is probably limited to those species which occur on gilled mushrooms or similar habitats in which two closely opposing surfaces are available for members of a mating pair to stand on.

It is not known whether females must mate on each mushroom before egg laying is initiated, or whether females previously mated on another mushroom can begin egg laying activities

immediately after colonization of a mushroom. This is important, especially for those species which live on gilled mushrooms, since the relatively short life of many gilled mushrooms may place severe constraints on time available for completion of life cycles.

Observations of oviposition by gyrophaenines have not been published. I have not observed this process, nor have I observed eggs of those species which live on polypores. Therefore, these comments are limited to those species which occur on gilled mushrooms. It is reasonable to assume that egg laying will be similar in those species which occur on polypores, but this remains to be verified.

Ashe (1981a) reported finding eggs of *P. fasciata* on specimens of a species of *Russula* (probably *R. foetans* (D.C. ex Fr.). The eggs were arranged in loose irregular clusters of four to 14 on the surface of the gills "with the long axis of the egg parallel to the gill surface." These eggs were ovoid, white, translucent, and measured 0.39 X 0.43 mm.

I have also observed eggs of *Gyrophaena* (*Phaenogyra*) *californica* Casey on a species of *Paxillus*. These eggs are similar to those of *P. fasciata* and were also found in loose clusters on the gills. These, however, were also found in loose rows at the base of the gills. Larvae hatched from the eggs of both species. Larvae from eggs of *P. fasciata* were reared to adults.

These observations are in contrast to those of White (1977: 307), who reports finding eggs of *Gyrophaena gentilis* Erichson "laid singly into the proximal margin of the gills of *Tricholmopsis rutilans* (Fr.) Sing.". This seems to imply that eggs are inserted individually into the gill margin near the base. This is different from egg positioning described above. This discrepancy cannot be reconciled at this time. However, White does not actually report having observed these eggs hatch into gyrophaenines. Also, since gyrophaenine females lack a sclerotized ovipositor, it is not clear how the eggs are inserted into the gill flesh.

Topp (1973) reported that adult females of *Bolitochara lunulata* Paykull and *Aleochara moerens* Gyllenhal take their eggs in their mandibles immediately after oviposition and deposit them in a suitable hiding place. Later (1975) he reported a similar activity among females of several athetine species and suggested that this may be a characteristic habit of aleocharines. It is not known if females of gyrophaenine species rearrange their eggs after oviposition.

Oviposition probably occurs very soon after colonization. Supporting this suggestion is the fact that Ashe (1981a) found eggs of *P. fasciata* on a mushroom which was being colonized. However, circumstantial observations made while retaining adults with fresh mushrooms suggest that there may often be a longer pre-oviposition period after colonization.

Ashe (1981a) has described eclosion in larvae of *P. fasciata*. Quick, jerking movements were observed within the chorion as early as an hour before eclosion. Eclosion is effected when the larva straightens its body and splits the chorion at the head end. The larva crawls free and the chorion collapses. Egg bursters have not been observed in instar I larvae of *P. fasciata*. Ashe (1981a) suggested that small teeth on the outer surface of the mandibles of instar I larvae of *P. fasciata* may serve to abrade the inner surface of the chorion during the quick, jerking movements which precede eclosion. However, egg bursters are present as small spines on the metanotum and abdominal tergum I of instar I larvae of many other gyrophaenines.

Ashe (1981a) reported that larvae of *P. fasciata* begin feeding immediately, often before completely free of the chorion. This rapid initiation of feeding activity after eclosion is probably typical of gyrophaenines which live on gilled mushrooms.

Based on circumstantial evidence, Ashe suggested that the incubation period of eggs of *P. fasciata* is about 24 hours at room temperature (22-24°C). The mushroom was being colonized at the time of collection, suggesting that adults had not been on the mushroom long.

All eggs hatched at very nearly the same time, and all eggs had hatched within 22 hours of collection. Eggs of most other gyrophaenines which occur on gilled mushrooms probably have incubation times which do not vary greatly from this.

Growth and development of gyrophaenine larvae is very rapid. Again, the only detailed data available for larval development are for *P. fasciata*. However, my observations incidental to rearing a number of species of *Gyrophaena* indicate that developmental times reported for *P. fasciata* are very similar to those of many other gyrophaenines — at least those which occur on gilled mushrooms.

Gyrophaenines have three larval instars. At room temperature larvae of *P. fasciata* completed instar I in an average of 14.2 hours, instar II in 14.8 hours and instar III (to the time the larva left the mushroom) in about two days. Thus the entire larval period on the mushroom occupied only about three days with the first two instars completed in about a day.

When instar III larvae are mature (at the end of about three days of larval life), they become restless and begin to crawl away from the mushrooms. These larvae push their way into cracks or interstices of the litter and soil and begin to form pupal cells.

While observations indicate that this description of larval development is true for most species which occur on gilled mushrooms, it is not known whether it also applies to larvae of those gyrophaenines which live on polypore mushrooms. The greater longevity of polypores, the fact that they do not produce spores in this abundance over such a short period of time as do gilled mushrooms, and the fact that polypores may produce spores sporadically rather than continuously, may seriously affect rates of larval development. Larvae of gyrophaenines which live on polypores may require much longer to develop than those which live on gilled mushrooms.

Pupal cell formation begins soon after a larva crawls into the soil.

Construction of pupal cells by larvae of *Gyrophaena nana* Paykull has been described by Ashe (1981b). After selection of a space between substrate particles, a larva begins to enlarge and shape it by rearrangement of the substrate particles with its mandibles. Silk is extruded as a clear, colorless droplet at the apex of the abdomen. This droplet is touched to the substrate and drawn out as a thin thread. Silken threads are used to bind substrate particles in position. Completion of the pupal cell requires 12-24 hours.

The completed pupal cell is ovoid or spheroid and consists of a mass of substrate particles held together by a loose to dense network of fine silk fibers. The center of this cell is occupied by a more or less densely woven cocoon within which the larva pupates. Pupal cells constructed in this way are probably typical of most aleocharines. After completion of the pupal cell the larva becomes inactive and shortens and thickens to form a prepupa. Ecdysis to the pupa occurs two or three days later.

Duration of the pupal stage varied from eight to 12 days for *P. fasciata*, but I have observed pupal stages as short as five days (*Gyrophaena nana*) and as long as 14 days (several species).

After ecdysis, most teneral adults remain in the pupal cell one or two days before emerging from the soil. Many adults are still teneral when they emerge from the soil, but are quite active and able to fly well even though sclerotization is incomplete. Probably these newly emerged adults colonize fresh mushrooms immediately if these are available. Teneral adults are fairly common on fresh mushrooms in late summer. However, they may become semi-dormant in leaf litter or under logs if fresh mushrooms are not available.

Because generation time is short, and newly emerged adults can immediately colonize fresh mushrooms, more than one generation per year is possible. Batten (1973) reported that

*Gyrophana gentilis* Erichson is bivoltine in Holland.

I do not know if number of generations per year is genetically determined for each species, or if number of generations per year is indeterminate and varies with length and climate of the growing season and with length of time fresh mushrooms are available.

While the above summary of a probable multivoltine life history seems correct for most species of *Gyrophana*, some may be obligatorily univoltine. A number of my attempts to rear larvae of several species of the *Gyrophana pulchella* species group (Seevers, 1951) have failed. Mature larvae of members of this group burrow into the soil and form pupal cells. However, I have not been able to get them to complete development to pupae. Larvae simply remain in pupal cells until they die one or two weeks later, which suggests that some essential requirement for pupation is not being supplied. This contrasts sharply with the ease with which other species of *Gyrophana* have been reared. While other hypotheses are possible, at present the most simple explanation for these observations is that members of the *G. pulchella* group require a diapause period, probably cold induced, to initiate pupation and subsequent development. If this is true then they are probably univoltine. While the hypothesis that members of the *G. pulchella* group are obligatorily univoltine requires confirmation, it suggests that other species of gyrophaenines may also have only a single generation per year.

Seasonal activity patterns of gyrophaenines are determined chiefly by fruiting cycles of mushrooms. In general, gyrophaenines may be active throughout the summer and early fall whenever mushrooms occur. However, individual species may have more restricted periods of activity, which for at least some species, seem to correspond primarily to appearance of a particular assemblage of mushrooms, probably including preferred host(s) of that species.

A particularly striking example of a restricted period of activity is illustrated by two years of observations of the habits of *Gyrophana simulans* Casey near College Station, Texas. In this area mushrooms are common from late spring until late fall following periods of wet weather. Gyrophaenines are found on mushrooms any time fruiting bodies occur, with specimens of most species present throughout the fruiting season. During the two seasons that I collected around College Station, adult specimens of *G. simulans* were very rarely encountered during most of the fruiting season. However, in mid- to late October, adults of this species began to appear in abundance on fruiting bodies of *Tricholoma* (prob. *T. sulfureum* Fries) which first fruited at that time. A large number of adults and larvae of *G. simulans* were found throughout the fruiting period of this mushroom. With cessation of fruiting of this species of *Tricholoma*, *G. simulans* virtually disappeared from the gyrophaenine fauna until the next October. Even during the time of maximum beetle activity, adults of *G. simulans* were seldom encountered on other mushrooms, at least in the College Station area. It is important to note that *G. simulans* occurs throughout the eastern United States. In most other areas it colonizes a much broader range of mushrooms than was observed in the study area. Consequently, in most areas, its seasonal activity period may be much longer.

Such apparent restricted periods of activity may reflect a collecting bias. However, this is almost certainly not always true, and a more or less seasonally restricted activity period seems to be the rule for a number of species of gyrophaenines.

As noted for *G. simulans* above, seasonal activity pattern for a species may vary geographically.

Mushrooms are often not present throughout the time when most gyrophaenine species are potentially active. Absence of fruiting bodies is especially apparent during dry periods. It is uncertain how the beetles respond to this situation. Few adults are found in moist or moldy leaf

litter or under logs during these periods. It seems likely that when suitable hosts are not available, adults enter the litter and become semi-dormant.

Because of the marked behavioral and morphological adaptations of gyrophaenines to feeding on the hymenium layer of mushrooms, it is unlikely that most of these beetles feed on fungus mycelium when they are found in moldy leaf litter or under fungus covered logs. This may not be true of those, such as species of *Encephalus* and *Brachida*, which appear to be normally found in these habitats.

It is not known how gyrophaenines coordinate their periods of activity to times when mushrooms are present. Most probably avoid the problem of very exact timing of adult activity by having a range of host preferences rather than being highly adapted to a single mushroom species. They may simply periodically search for mushrooms then become inactive again if suitable mushrooms are not found. On the other hand, they may become active in response to environmental cues. Since many fungi commonly form fruiting bodies following periods of wet weather, increase in moisture is a possible general cue for gyrophaenines to become active. Many gyrophaenines may profitably occupy a range of different mushrooms, so that such general cues may be sufficient. However, many mushrooms are quite seasonal in occurrence. Those species of gyrophaenines which have a restricted range of host preferences may require more specific cues to allow timing of activity periods to the proper season.

*Discussion of life cycle.*— Evolution of ability to eat maturing spores, basidia and cystidia of the hymenium layer is a major evolutionary innovation for gyrophaenines. This ability opened a new adaptive zone within the mushroom habitat which provided an abundant and virtually unexploited, but highly unpredictable resource. However, the requirement for a fresh and active hymenium layer for both larval and adult survival imposes a number of constraints on the life history of gyrophaenines. Many of the features of the life cycle are a response to the unique characteristics of the mushroom as a habitat.

For gyrophaenines the most important general characteristics of the mushroom habitat are that mushrooms are: 1) ephemeral (often highly so); 2) unpredictable in time and space; and 3) highly heterogeneous in physical and chemical characteristics. Exploitation of habitats with these characteristics requires adaptation to: 1) an efficient host finding mechanism; 2) rapid larval development; and 3) some means of surviving when suitable mushrooms are not available.

Because both adults and larvae of gyrophaenines probably feed exclusively on the active hymenium layer of mushrooms, they occur only on fresh mushrooms. Decaying mushrooms are not suitable habitats for these beetles and are soon colonized by other species of staphylinids which are probably predaceous. Among mushrooms inhabited by gyrophaenines, time from first spore production until the mushroom becomes unsuitable as a habitat varies considerably depending on a number of factors including particular species of mushroom; temperature, humidity and rainfall; and how extensively the mushroom is attacked by other insects, particularly fly larvae. The period that a mushroom remains a suitable habitat for gyrophaenines may vary from as little as a week for some gilled mushrooms to a month or more for woody polypores.

Mating, oviposition and larval development must take place on a single mushroom. Apparently larvae leave the mushroom only to pupate. It is unlikely that any larvae survive if the mushroom which they inhabit is destroyed or decays before they are mature.

This is a serious constraint, especially for those gyrophaenines which occupy short-lived gilled mushrooms. Efficient host finding, rapid colonization and oviposition, short incubation

period of eggs and very rapid larval development are undoubtedly adaptations to the ephemeral nature of these mushrooms.

However, in many characteristics which are important to gyrophaenines, gilled and polypore mushrooms are quite different habitats. Unfortunately, as noted above, no details are known of the life history of those gyrophaenines which occur on polypore mushrooms. However, at least potentially, responses to the different conditions of these two major mushroom types could produce marked differences in the life cycle and population structure of the gyrophaenines which occupy them.

One of the most obvious differences between the two types of mushrooms is length of time that each is present in the environment. Gilled mushrooms are commonly short-lived, many decaying within a few days to a week. In contrast, polypores, especially woody species, may persist for several weeks to a month or more. It seems reasonable to expect that those gyrophaenines which live on persistent polypores are under less stringent requirements for a very rapid life cycle than those which live on gilled mushrooms.

Another potentially important difference is availability and production rate of hymenium tissue of the two groups of mushrooms. Gilled mushrooms have a very active hymenium layer, producing great quantities of spores during a relatively short period of time. Since the hymenium layer is on the surface of the gills, and the gyrophaenines actually live between the gills, the beetles have an abundance of readily available food constantly throughout the life cycle. The hymenium layer of polypores, on the other hand, is formed inside pores, many of which are too small for a beetle to enter. Also, polypores produce spores for a much longer period, though spore production throughout this period may not be constant. Many polypores produce spores periodically, often in response to wet weather. This periodic production of spores and relative isolation of beetles from direct contact with the hymenium layer may have effects on both life cycle and feeding habits of members of those species which inhabit polypores.

Possibly, gyrophaenines which habitually live on more persistent woody polypores may colonize more slowly, mate and oviposit for a more extended period, have a longer larval period, and have adults and larvae overlapping occupancy of the same mushroom for a more extended period. Observations about natural history of those gyrophaenines which are obligatory inhabitants of persistent polypores are required to test these suppositions.

Polypores may not be as productive a habitat as are gilled mushrooms, because one seldom finds very large numbers of individual beetles per mushroom on persistent polypores.

An interesting possibility is that feeding and life cycle requirements imposed on gyrophaenines by the extremes of these two general types of mushroom habitats makes it difficult for beetles to change from one type to the other. Thus the broad host trends displayed by members of gyrophaenine taxa which are restricted to either polypores or gilled mushrooms respectively may be reinforced by the difficulty which members adapted to one group experience in surviving on the other.

Although differences in general habitat features between persistent polypores and very ephemeral gilled mushrooms are quite striking, these extremes are connected by a range of habitats of more or less short-lived polypores and more or less persistent gilled mushrooms. Mushrooms which exhibit intermediate general characteristics provide a bridge or "transition zone" (Bock, 1965) of habitats between these two extremes. This transition zone has probably been very important in evolution and diversification of gyrophaenines in the various mushroom groups.

### Interactions with other mushroom-inhabiting insects

Detailed observations have not been published about how gyrophaenines interact with other insects which occupy mushrooms. However, several interesting hypotheses about the broad, general characteristics of these interactions can be inferred from a comparison of the ways that gyrophaenines and other insects use the mushroom habitat.

Evolution of the ability to feed exclusively on the spore producing tissues of mushrooms is the key innovation which opened the mushroom habitat to gyrophaenines. This particular way of using mushrooms fundamentally affects relationships with other mushroom-inhabiting insects.

The habit of eating mushroom spores is limited to a few groups of relatively small insects and includes ptiliid beetles (subfamily Nanosellinae, Dybas, 1976), some Collembola, and members of some families of Acarina. Lawrence and Newton (1980) discuss many groups of insects which eat spores and fruiting bodies of slime molds (Myxomycetes).

Gyrophaenines differ from other insects which eat spore tissue in that they are relatively large (in relation to the tissue they consume), and they do not eat only mature spores. Instead, they are capable of feeding on both maturing spores and also the hyphal structures of the hymenium layer of gilled and polypore mushrooms. Therefore, gyrophaenines eat both spores and spore producing tissue.

In addition, most arthropods which inhabit mushrooms eat, not the hymenium layer, but the context tissue of gills, caps or stems.

Thus, it appears that there is little direct competition for this food resource within the mushroom habitat. However, because of the large number of animals, particularly arthropods, which use mushrooms, indirect competition may be very important to gyrophaenines. Any animal whose activities reduce or destroy the ability of a mushroom to produce a hymenium layer is in indirect competition with gyrophaenines.

A number of arthropods eat the flesh of the gills, or the context of the cap. These include larvae and adults of several species of erotyid beetles (including *Triplax* Herbst and *Tritoma* Fabricius species) (Arnett, 1968), both adults and larvae of some scaphidiid beetles (Arnett, 1968, and personal observations), *Oxyporus* Fabricius adults and larvae (Campbell, 1969, and personal observations), and some nitidulid beetles (Arnett, 1968). Activities of fly larvae are particularly important in gilled fungi. Large numbers of these burrow in the cap, stem and gills, extensively damaging the mushroom, especially as larvae begin to mature. In addition, some slugs often feed on the gills and caps of mushrooms. Even if feeding activities of an animal on the mushroom do not directly affect the gills, the trauma caused to the mushroom tissue may accelerate rotting of the fruiting body. Scheerpelz and Höfler (1948) pointed out the dramatic hastening of rot caused by feeding activities of fly larvae within caps of gilled mushrooms.

In general, activities of other arthropods on polypores are probably of less importance to gyrophaenines than on gilled mushrooms. However, feeding on the pore surface may reduce the reproductive capability of a polypore. Adults of some erotyid beetles, such as members of *Dacne* Latreille and *Megalodacne* Crotch (personal observations) feed extensively on the pore surface, while larvae burrow into the pore layer. Some scaphidiid and tenebrionid beetles have similar habits. Slugs may also be important in destruction of the pore surface at certain times. Other beetles (and in softer polypores, fly larvae) may burrow into the context of the fruiting body, ultimately destroying it. These include, most importantly, tenebrionid beetles such as *Bolitotherus cornutus* (Panzer) and *Diaperus maculata* Oliver.

Many important inhabitants of polypores, such as ciid beetles, generally colonize fruiting bodies after spore production has ceased (Lawrence, 1973; Paviour-Smith, 1960a) and probably have little effect on gyrophaenines.

Since gyrophaenines usually colonize a mushroom very soon after spore production begins (at least for those that live on gilled mushrooms), they probably normally avoid interaction with many of the predaceous and saprophytic beetles (mainly staphylinids) which colonize the later stages of fruiting bodies. The presence of late instar gyrophaenine larvae may overlap colonization of mushrooms by these later inhabitants, so it is possible that gyrophaenine larvae may be preyed upon by these predators. However, this predation has not been observed. It would be very surprising if gyrophaenine larvae do not form a food source for some predators, since they may be very abundant on more mature mushrooms. In this regard, the very well developed glandular process on tergum 8 of gyrophaenine larvae may be important. Moore, Legner and Badgley (1975) showed that a similar gland in larvae of *Oligota oviformis* Casey acted as an osmeterium and suggested that it may have a defensive function. Use of the tergal gland has not been investigated in gyrophaenine larvae.

### PERSPECTIVES ON CLASSIFICATION

Development of a general purpose classification of organisms is one of the most important tasks of systematists. Several recent works (Eldredge and Cracraft, 1980; Wiley, 1981; Mayr, 1981; and included references) have discussed in detail the philosophical, methodological and historical base of biological classifications. These need not be reviewed in detail here.

I agree with Mayr (1981) that a classification must serve as a basis for an information and retrieval system, and also as a basis for biological generalizations. Most systematists agree that a classification based on evolutionary patterns is most convenient for biological organisms. In order to most completely meet these requirements, as much evolutionary information as possible should be included in the classification. However, Eldredge and Cracraft (1980) have correctly pointed out that if the Linnaean hierarchy is used as the system for classification, then the only information actually contained within the structure of the classification itself is the hierarchical arrangement of taxa. This hierarchical structure, then, is the only information which can be extracted from the classification without addition of conventions or explanations. The Linnaean hierarchy is particularly suited as a classification system because the genealogical structure of taxa is hierarchical. This hierarchical structure of genealogical relationships is hypothesized in a cladogram. "Cladistic" classifications transfer information directly and unaltered from a cladogram to a classification, so that each strictly monophyletic group is given a categorical rank in the classification, and the hierarchical structure of the cladogram is directly reflected in hierarchical structure of these categorical ranks. In this system, all evolutionary information (genealogy) put into the classification is directly retrievable from the structure of the classification itself.

The major contending classification system is called an "evolutionary" classification. Proponents of this method argue that the most generally useful classification includes not only cladistic (genealogical) relationships, but also information on degree of similarity of organisms included in each taxon (patristic relationships). This often leads to recognition of paraphyletic groups within a classification. While paraphyletic groups can contain very useful information, particularly ecological, structural and developmental similarity of included taxa, addition of such information to a classification results in loss of genealogical information. That is, since



hierarchical structure is the only information inherent in the classification, the genealogical relationship between the paraphyletic group and the monophyletic group derived from it cannot be recognized. Additionally, if both patristic and cladistic relationships are included, then it becomes impossible to determine which is being reflected at any one point in the classification. Finally, since patristic relationships are not hierarchical in the same sense that genealogical relationships are, patristic relationships cannot be suitably reflected by the hierarchical structure of the Linnaean system. Despite these problems with evolutionary classification, there are times when information about patristic relationships are more valuable for comparison than is information about genealogical relationships.

Because of the nature of the Linnaean hierarchy itself, I prefer a classification which is cladistic in that all included taxa are strictly monophyletic. Patristic information can be expressed by convention or explanation of taxa within the classification.

In addition to the uses of a classification mentioned above, a classification must act as a vehicle for communication of information about organisms. To perform this function a classification must have a certain amount of stability.

This requirement for effective communication and stability in a classification has been, in part, the reason that I have taken a conservative approach to reclassification of gyrophaenine genera in this treatment. The gyrophaenines are one of the few major groups of aleocharines for which a relatively large number of character state distributions have been analyzed. Analysis of other groups of aleocharines may ultimately result in major changes in character analysis of states in gyrophaenines. It is, therefore, possible that hypotheses about relationships of gyrophaenine genera will require slight to considerable modification. Therefore, I have retained all genus-level names which have been proposed as long as the group can be hypothesized to be monophyletic. This requires that monophyletic lineages of similar external structure be given generic rank, and has resulted, for example, in splitting *Agaricomorpha* n. gen. from *Agaricochara* Kraatz though they are similar externally. This also has resulted in a situation in which the genus-level diversity within taxa of the "*Sternotropa*" lineage is not much greater than that among species-group level taxa within *Gyrophaena*. The "*Sternotropa*" lineage may include too many genus-level taxa. Alternatively, *Gyrophaena* is an exceptionally diverse group of organisms, and may include several monophyletic lineages, each of which deserve generic rank.

I believe that proposal of a more rigorous cladistic classification of gyrophaenines, or any large group of aleocharines, is premature at this time. Many changes in classification of aleocharines can be expected as knowledge of relationships increases. Major revisions in classification before other aleocharines are better known are likely to lead to instability and confusion later.

## TAXA OF GYROPHAENINES EXAMINED

This section is primarily intended as documentation of materials which were critically surveyed in establishing generic descriptions and character distributions for phylogenetic analysis. For reasons outlined above, it is not intended as a catalogue of gyrophaenines. Therefore, this table only lists those species for which specimens were examined in some detail (that is, examined, either whole or dissected, with compound optics or the scanning electron microscope). Specimens of a large number of additional species, especially in the genera *Gyrophaena*, *Phanerota*, *Eumicrota*, *Brachida*, *Sternotropa* and *Agaricomorpha*, were examined in less

detail.

The letters 'T' and 'S' following each species name indicate whether primary type material (holotype, paratype or syntype) or other identified specimens respectively were examined. A brief summary of the known distribution of each species is given. In this table, genera are listed in the order in which they appear in the descriptive section, and species are alphabetically ordered under each genus.

*Gyrophæna* Mannerheim 1830:488

<i>affinis</i> Sahlberg	T,S	USA, Canada
<i>antennalis</i> Casey	T,S	e USA, Canada
<i>blackwelderi</i> Seevers	S	e USA
( <i>Agaricophæna</i> ) <i>boleti</i> (Linnaeus)	S	Europe
( <i>Phaenogyra</i> ) <i>californica</i> Casey	T,S	w USA
( <i>Enkentrophæna</i> ) <i>championi</i> Cameron	S	India
<i>chippewa</i> Casey	T,S	e USA
<i>coniciventrìs</i> Casey	T,S	e USA
<i>egena</i> Casey	T,S	e USA
<i>frosti</i> Seevers	T,S	e USA
<i>gilvicollis</i> Casey	T,S	n, e USA, Canada
( <i>Phaenogyra</i> ) <i>gracilis</i> Seevers	T,S	n USA, Canada
<i>hubbardi</i> Seevers	S	se USA
<i>nana</i> (Paykull)	S	n USA, Canada, Europe
<i>nanoides</i> Seevers	T,S	e USA, Canada
( <i>Enkentrophæna</i> ) <i>plicata</i> (Fauvel)	S	Seychelles
<i>pollens</i> Sharp	T	Panama
( <i>Orphnebioidea</i> ) <i>rosti</i> Schubert	S	India
<i>sculptipennis</i> Casey	T,S	e USA
<i>spatulata</i> Seevers	T,S	sw USA
( <i>Phaenogyra</i> ) <i>strictula</i> Erichson	S	Europe
( <i>Phaenogyra</i> ) <i>subnitens</i> Casey	T,S	ne USA
( <i>Orphnebioidea</i> ) <i>tuberculiventrìs</i> (Bernhauer)	S	India
<i>vitrina</i> Casey	T,S	e USA
undes. sp. 1	S	e USA
undes. sp. 2	S	Mexico
undes. sp. 3	S	Mexico
undes. sp. 4	S	Mexico
undes. sp. 5	S	Guatemala

*Phanerota* Casey 1906:285

( <i>Acanthophæna</i> ) <i>appendiculata</i> (Motschulsky)	S	India, Malaya
<i>carinata</i> Seevers	T,S	se USA
<i>dissimilis</i> (Erichson)	S	e USA
<i>fasciata</i> (Say)	S	e USA
( <i>Acanthophæna</i> ) <i>insigniventrìs</i> (Cameron)	S	India
( <i>Acanthophæna</i> ) <i>lamellata</i> (Cameron)	S	New Hebrides

undes. sp. 1	S	Mexico
undes. sp. 2	S	Guatemala
<i>Eumicrota</i> Casey 1906:280		
<i>atomaria</i> (Cameron) (from <i>Gyrophaena</i> )	T	West Indies
<i>corruscula</i> (Erichson)	S	e USA
<i>minutissima</i> Casey	S	se USA
<i>socia</i> (Erichson)	S	e USA
<i>spinosa</i> Seevers	T,S	sw USA
<i>varians</i> (Sharp) (from <i>Gyrophaena</i> )	T	Guatemala
undes. sp. 1	S	sw USA
undes. sp. 2	S	Mexico
undes. sp. 3	S	Mexico
undes. sp. 4	S	Mexico
undes. sp. 5	S	Guatemala
undes. sp. 6	S	Mexico
<i>Encephalus</i> Kirby 1832:163		
<i>americanus</i> Seevers	S	n USA
<i>complicans</i> Kirby	S	Europe
<i>laetulus</i> Broun	T	New Zealand
<i>zealandicus</i> Cameron	T	New Zealand
<i>Probrachida</i> new genus		
<i>carinata</i> (Sharp)	T	Guatemala
<i>geniculata</i> (Sharp)	T	Panama
<i>modesta</i> (Sharp)	T	Panama
<i>reyi</i> (Sharp)	T	Amazon
<i>sparsa</i> (Sharp)	T	Guatemala
undes. sp. 1	S	Mexico
<i>Brachida</i> Mulsant and Rey 1872:94		
<i>africana</i> Bernhauer	T,S	Natal
<i>densiventris</i> Bernhauer	T,S	South Africa
<i>exigua</i> Heer	S	Europe
<i>natalensis</i> Bernhauer	T,S	Natal
<i>notha</i> (Erichson)	S	Europe
<i>sublaevipennis</i> Cameron	T,S	Bengal
<i>Agaricochara</i> Kraatz 1856:361		
<i>aspera</i> Fauvel	S	Europe
<i>laevicollis</i> Kraatz	S	Europe
<i>Sternotropa</i> Cameron 1920b:220		
<i>apicalis</i> Cameron	T	India
<i>brevicornis</i> Cameron	T,S	Fiji

<i>elevata</i> (Fauvel) (from <i>Brachida</i> )	S	Fiji
<i>flavicornis</i> Cameron	T,S	Malaya
<i>longicornis</i> Cameron	T	Fiji
<i>nigra</i> Cameron	T	Singapore
<i>Pseudoligota</i> Cameron 1920b:213		
<i>affinis</i> Cameron	T,S	India
<i>karyni</i> Cameron	T,S	India
<i>robusta</i> Cameron	T,S	Malaya
<i>varians</i> Cameron	T,S	Singapore
<i>Neobrachida</i> Cameron 1920a:51		
<i>castanea</i> Cameron	T	Ceylon
<i>Adelarthra</i> Cameron 1920b:222		
<i>barbari</i> Cameron	T	Singapore
<i>Brachychara</i> Sharp 1883:267		
<i>aterrima</i> Cameron	T	West Indies
<i>brevicornis</i> Sharp	T	Guatemala
<i>crassa</i> Sharp	T	Guatemala
sp. (prob. <i>crassa</i> Sharp)	S	Mexico
undes. sp. 1	S	Mexico
undes. sp. 2	S	Mexico
<i>Agaricomorpha</i> new genus		
<i>apacheana</i> Seevers	S	sw USA
undes. sp. 1	S	Mexico
undes. sp. 2	S	Mexico
undes. sp. 3	S	Canada
undes. sp. 4	S	Mexico
undes. sp. 5	S	Panama
undes. sp. 6	S	Guatemala

DESCRIPTION AND RECLASSIFICATION OF WORLD GENERA OF  
GYROPHAENINA

Subtribe GYROPHAENINA

- Gyrophaenini (Eurypalpi) Kraatz 1858:352
- Gyrophaenides Thomson 1860:266
- Gyrophaenae Fauvel 1875:629
- Gyrophaenae Casey 1906:275
- Gyrophaenae Fenyés 1918-21:18
- Gyrophaenini Fenyés 1921:34
- Gyrophaenae Seevers 1951:670
- Gyrophaenina Arnett 1968:285
- Gyrophaenini Lohse 1974:25
- Gyrophaenae Seevers 1978:161

**Diagnostic Combination.**— Adults of subtribe Gyrophaenina are recognized by the combination of 4,4,5 tarsal formula, nonstyliform labial palpi, broadly separated middle coxae, broad meso- and metasternal processes not joined by an isthmus but meeting along a broad suture, truncate lacinial apex with well developed spinose area (spore brush), reduced spines and setae on inner face of lacinia, four well separated rows of flattened setae on apex of galea in most, and a plate-like flange on neck of spermatheca.

**Description.**— Body length 0.6 to 3.5 mm. Body form and color various.

**Head.** Infraorbital carina well developed, complete or reduced antero-laterally. With or without additional carina from dorso-lateral base of neck to gular sutures. Neck absent. Gula with sutures more or less widely separated. Eyes medium sized to very large. Antenna 11-articled. Labrum with major setae well developed, with or without additional setae; medial sensilla area well developed; lateral sensillum row with three to five sensilla, at or more or less distant from lateral margin, sensilla well developed or reduced. Maxillary palpus four-articled. Lacinia with apex obliquely truncate with more or less dense patch of teeth (Figure 73); inner face without teeth or spines (in most) or with few scattered teeth, setae in single row (in most) or loosely scattered to moderately dense. Galea with apical setae more or less flattened, in four distinct rows (in most), or unmodified and in five to 13 rows. Mandibles more or less robust; apices simple, or left, and in some also right, mandible bifid at tip; right mandible with slightly to well developed molar tooth. Prostheca well developed, membranous. Labial palpus two-articled, not styliform. Ligula various. Medial setae of labium two, or, in most, one.

**Thorax.** Pronotum transverse to broadly rounded; posterior margin bisinuate to broadly rounded. Hypomera visible or not in lateral aspect. Elytral apical angles markedly to not sinuate. Prosternal peritremes behind procoxae absent, procoxal cavities broadly open. Mesosternum with carina complete, incomplete, reduced to low ridge, or non-carinate. Mesosternal process broad, extended between middle coxae to contact metasternal process along broadly rounded or truncate juncture; juncture suture complete, fused or more or less beaded. Isthmus absent, mesosternal process extended to middle or base of middle coxae. Middle coxae widely separated. Tarsal formula 4-4-5.

**Abdomen.** Abdominal segments 3 to 7 more or less deeply transversely impressed to 3 to 5 slightly impressed. Tergum 7 with abdominal gland openings on anterior margin.

**Male genitalia.** Median lobe and parameres varied. Flagellum large, tubular, slightly to moderately sclerotized. Median lobe without complex internal structure of eversible membrane, hooks and spines in most. Apical process extensively modified or not.

**Female genitalia.** Neck of spermatheca with lateral flange-like plate. Spermatheca simple (Figure 176) or neck elongate distal (Figure 185) or proximal (Figure 179) to lateral flange.

**Larvae.**— Because structural variation among aleocharine larvae is very inadequately known, it is inappropriate to give a full description of gyrophaenine larvae at this time. The following diagnosis is given to aid identification.

Among aleocharine larvae, gyrophaenine larvae are recognized by the obliquely truncate mala with numerous, more or less closely spaced teeth; spine-like sensory appendage on penultimate antennomere; large, well developed abdominal gland on tergum 8, with a pair of brush-like setae dorsally near apical margin; and the association with fresh mushrooms.

Few detailed studies of larvae of gyrophaenines have been published. These are discussed under the appropriate genus.

I have examined probable larvae of species representing seven genera of gyrophaenines: *Agaricochara*, *Agaricomorpha*, *Brachychara*, *Eumicrota*, *Gyrophaena*, *Phanerota* and *Pseudoligota*. These larvae have a number of characteristics in common. The mala of the maxilla is truncate and covered with numerous, more or less closely spaced teeth (Figures 240, 242, 243). Number and spacing of these teeth vary considerably among species and genera. Similarity of this structure to the spore brush on the apex of the lacinia of adult gyrophaenines is striking.

In all gyrophaenine larvae examined, the outer apex of the maxilla has a small bifid plate-like structure which forms a cup over the more distal teeth of the mala (Figure 241). Ashe (1981a) suggested that this structure is a modified seta, but with closer examination, it seems more likely to be a scale-like cuticular modification. This interpretation is given support by additional plate-like structures on the apico-lateral side of the mala of larvae of *Brachychara* species (Figure 243) which appear to have been derived in a similar way to the

apical bifid plate. This structure may perform a function in larval feeding similar to that of the rows of plate-like setae on the galea of adult gyrophaenines.

Convergence in mouthpart structure between adult and larval gyrophaenines is evidence that adult and larval gyrophaenines are using resources of the mushroom habitat in the same way.

One important difference in mouthpart structure between adult and larval gyrophaenines is that larvae have sickle-shaped mandibles which lack the well developed, toothed molar region of adults. It is not known how this difference affects mandibular function.

Of particular interest is a brush-like seta on each side of the midline dorsally near the apex of the abdominal tergal gland on segment 8 (Figure 232). These were first described by White (1977) in larvae of *Gyrophaena gentilis* Erichson. Ashe (1981a) described similar setae in larvae of *Phanerota fasciata* (Say), and pointed out that similar setae were present on tergum 8 of all gyrophaenine larvae which he had examined. However, White (1977) had reported that he was unable to find the setae on larvae of *Agaricochara* species which he had examined. Ashe (1981a) suggested that he over-looked these structures in these species. I have since examined larvae of *Agaricochara laevis* Kraatz and identified these setae, which are very small and spatulate rather than brush-like (similar to those of larvae of *Agaricomorpha apacheana*, Figure 244). No similar structures have been described or are known to me in other aleocharine larvae. A reasonable hypothesis is that complex structure of the maxilla of larval gyrophaenines and presence of brush-like setae dorsally on abdominal tergum 8 are uniquely derived with the Gyrophaenina. These character states then, are autapomorphies, and offer further support that the subtribe as here defined is monophyletic.

*Discussion and Reclassification.*— The subtribe Gyrophaenina has been differently defined and placed at different formal ranks by different authors. The first to recognize these beetles as a distinct group was Kraatz (1858). In his Subdivision II, the Gyrophaenini (Eurypalpi), he recognized three genera: *Encephalus* Westwood, *Gyrophaena* Mannerheim, and *Agaricochara* Kraatz. Thomson (1860, 1867) was first to rank it as a subtribe, the Gyrophaenides, and included *Encephalus* and *Gyrophaena*. Fauvel (1875) returned to the arrangement of Kraatz (1858) with the Gyrophaenae as Section II of the Aleocharinae. Within the Gyrophaenae he included *Gyrophaena*, *Encephalus* and *Brachida* Mulsant and Rey.

Casey (1906) recognized eight genera in the subtribe Gyrophaenae, including, in addition to all genera previously recognized, *Diestota* Rey, *Phaenogyra* Mulsant and Rey, and two new genera, *Eumicrota* Casey and *Phanerota* Casey. Fenyés (1918-21) recognized seven genera in his "Group Gyrophaenae". He did not include *Diestota* and ranked *Phanerota*, *Eumicrota* and *Phaenogyra* as subgenera of *Gyrophaena*. He also included *Brachychara* Sharp, *Hoplomicra* Sharp and *Hygropetra* Motschulsky. Increase in number of genera in the subtribe continued until Bernhauer and Scheerpeltz (1926) and Scheerpeltz (1934) listed 23 genera within subtribe Gyrophaenae. Seevers (1951) was more conservative and recognized only *Gyrophaena*, *Phanerota*, *Encephalus* and *Brachida* within the Holarctic fauna. He ranked *Eumicrota* and *Agaricochara* as subgenera of *Gyrophaena*, but later (1978) recognized these as distinct genera.

Many major workers on aleocharines have not placed these beetles in a distinct subtribe, but have included them within the tribe Bolitocharini or its equivalent. These include Mulsant and Rey (1871-75), Sharp (1883-87), Ganglbauer (1895) and Cameron (1920b, 1939).

In this revision I recognize 13 genera in the subtribe Gyrophaenina. These are:

*Gyrophaena* Mannerheim, 1830

*Phanerota* Casey, 1906

*Eumicrota* Casey, 1906

*Encephalus* Kirby, 1832

*Probrachida* new genus

*Brachida* Mulsant and Rey 1872

*Agaricochara* Kraatz, 1856

*Sternotropa* Cameron, 1920b

*Pseudoligota* Cameron, 1920b

*Neobrachida* Cameron, 1920a

*Adelarthra* Cameron, 1920b

*Agaricomorpha* new genus

*Brachychara* Sharp 1883

Members of these genera are similar in a number of characteristics. I believe that two of these, maxillary structure and a plate-like flange on the neck of the spermatheca, provide evidence for monophyly (see Phylogenetic Analysis for discussion).

The reasons for proposing subtribal rank include the conservative approach to classification of aleocharines in accordance with the discussion above. Also, it helps to indicate that the Gyrophaenina is probably a part of a monophyletic lineage of several similarly monophyletic "subtribes" within the tribe Bolitocharini. Evidence for this is the proposed sister group relationship of the Gyrophaenina with the subtribe Bolitocharina.

## IDENTIFICATION OF THE WORLD GENERA OF GYROPHAENINA

The following key is intended for identification of the known genera of the Gyrophaenina of the world. Relative positions of genera within the key imply nothing about relationships. Any similarity of various aspects of the key to lineages in the cladogram is an incidental result of relative usefulness of phylogenetically important characters as "key" characters.

Lohse (1974) pointed out that mouthparts are most useful for delimiting higher taxa among aleocharines. However, because of difficulty of observing mouthpart structure, his key is based on other characters. I prefer to use easily seen characters as important key characters, but the most reliable characters for arranging the genera of gyrophaenines in groups are those of the mouthparts, particularly structure of the ligula. Though Seevers (1978) states that structure of the ligula is not as reliable for classification of aleocharines as has been implied by its use in the past, such characters appear quite stable within genera or supergeneric taxa among gyrophaenines. Therefore, I have used form of this structure near the beginning of the key. Ligulae are very difficult to observe in many gyrophaenines, especially very small specimens. However, once observed, the structure provides unambiguous entrance into the proper part of the key. Other characters provided aid in identification of gyrophaenines when ligula structure cannot be observed. However, states of these characters are more variable and qualitative, and more subject to interpretation, and must be used with caution.

To my knowledge, structure and form of the setal patch on tergum 10 has not been previously used to identify aleocharines. Among gyrophaenines this is very useful, though it is difficult to observe if the abdomen is contracted. Because of overlap in external structure, specimens of a few gyrophaenine genera are most reliably identified by aedeagal or spermathecal features. I have used aedeagal structure as a major key character for separation of *Probrachida* and *Brachida*, and as a secondary character for identification of *Agaricomorpha*. In all of these genera, form of the median lobe is quite distinctive.

In uncertain identifications, geographical range of a genus is useful. Therefore, known ranges of members of each genus are given in the key. Differences in useful key characters between specimens of Holarctic and New Zealand *Encephalus* make it most useful to key them out in separate couplets. This division also helps emphasize that these two groups presently

placed in *Encephalus* may not belong to the same genus (see discussion under that genus).

Reliable identification of genera of gyrophaenines, and indeed of most aleocharines, is difficult. This results primarily from small size of the beetles and consequent difficulty in observing reliable key characters. Confident identification requires softening, clearing and dissection of many beetles, and observation under high magnification. Reluctance to use characters which require such specialized handling for identification is, at least in part, a cause of the present difficulty and uncertain reliability of most available keys. Aleocharines of such small size cannot be effectively handled using techniques appropriate to larger beetles.

**Key for the Identification of the Known Genera of Subtribe Gyrophaenina of the World**

- 1      Ligula broadly rounded (Figures 103, 105–109). Pronotum hind margins not or slightly bisinuate. Elytral apico-lateral angles not or, at most, slightly sinuate ..... 2
- 1'     Ligula more or less protruded and parallel-sided, entire (Figure 98) or bifid (Figure 111). Pronotum hind margins markedly, slightly, or not bisinuate. Elytral apico-lateral angles markedly, slightly, or not sinuate ..... 4
- 2 (1) Body markedly robust, broadly oval in dorsal aspect. Microsetae sparse, body subglabrous. Head deflexed and in more or less vertical plane, base covered by anterior margin of pronotum. Mesosternum in more or less vertical plane. Holarctic region ..... *Encephalus* Kirby (part), p. 250
- 2'     Body moderately to slightly robust, elongate-oval to more or less parallel-sided in dorsal aspect. Microsetae very to moderately dense, body pubescent. Head slightly or not deflexed, base slightly or not covered by anterior margin of pronotum. Mesosternum not in vertical plane ..... 3
- 3 (2') Labium with two medial setae. Without pair of macrosetae on vertex of head. Aedeagus distinctive; apical process of median lobe not highly modified; flagellum exerted, long, whip-like, not coiled inside basal capsule (Figures 202, 203). New World tropics. ... *Probrachida* new genus, p. 252
- 3'     Labium with one medial seta. With pair of macrosetae on vertex of head (Figure 15). Aedeagus distinctive; apical process of median lobe modified or not; flagellum not exerted, coiled inside basal capsule (Figures 204–206). Old World ..... *Brachida* Mulsant and Rey, p. 254
- 4 (1') Ligula bifid in at least apical 1/3. Hypomera not (in most) or slightly visible in lateral aspect. Mesosternum carinate or not ..... 5
- 4'     Ligula entire, more or less protruded and parallel sided (Figure 98) or slightly tapered to apex (Figure 100). Hypomera not visible or slightly or entirely visible in lateral aspect. Mesosternum carinate in apical 2/3 or not carinate (in most) ..... 11
- 5 (4) Body subglabrous. Lateral macrosetae on prothorax, elytra and abdomen extremely prominent, large, dark and bristle-like (Figure 231). Southeast Asia ..... *Adelarthra* Cameron, p. 260
- 5'     Body markedly to moderately pubescent. Lateral macrosetae of prothorax, elytra and abdomen not extremely prominent, or, if enlarged, not markedly so and limited to prothorax and/or elytra ..... 6
- 6 (5') Ligula as long as labial palpomere 1, bifid in apical 1/3 (Figure 115).



- Southeast Asia ..... *Neobrachida* Cameron, p. 259
- 6' Ligula shorter than labial palpomere 1, bifid at least 1/2 distance to base .... 7
- 7 (6') Setal patch on tergum 10 more or less square, not incised posteriorly to form a chevron-shaped patch ..... 8
- 7' Setal patch on tergum 10 incised posteriorly to form a chevron-shaped patch, or patch of one to three distinct rows of setae ..... 9
- 8 (7) Mesosternal and metasternal processes fused, suture indistinguishable. Southeast Asia, India ..... *Pseudoligota* Cameron, p. 258
- 8' Mesosternal and metasternal processes not fused, suture distinct. Palearctic region ..... *Agaricochara* Kraatz, p. 255
- 9 (7') Setal patch on tergum 10 chevron-shaped (Figure 175), but setae not in one to three distinct rows. Aedeagus distinctive, apical lobe laterally displaced from flagellum insertion (Figures 214, 215). Nearctic, Neotropical regions ..... *Agaricomorpha* new genus, p. 263
- 9' Setal patch on tergum 10 in one to three distinct chevron-shaped rows (Figures 170, 171, 174). Aedeagus not as above ..... 10
- 10 (9') Body form very robust, broadly oval in cross section. Mesosternum either not carinate or with low diffuse ridge medially. Head moderately deflexed into vertical plane. Mexico, Central America, West Indies ..... *Brachychara* Sharp, p. 261
- 10' Body form not robust, more or less flattened in cross section. Head not or slightly deflexed into vertical plane. Southeast Asia, India ..... *Sternotropa* Cameron, p. 257
- 11 (4') Mesosternum carinate in at least anterior 2/3. Body very robust, broadly oval in dorsal aspect. Elytral apico-lateral angle markedly sinuate. New Zealand ..... *Encephalus* Kirby (part), p. 250
- 11' Mesosternum not carinate. Body moderately robust to not robust, elongate oval to parallel-sided in dorsal aspect. Elytral apico-lateral angle moderately to not sinuate ..... 12
- 12 (11') Setal patch on tergum 10 in distinct V-shaped row (Figure 166). Prothorax markedly transverse, twice as wide as long or wider. Body of most specimens moderately to very pubescent. Antennae of most specimens short, with antennomeres 4 to 10 markedly transverse, in form of loose parallel-sided club (Figure 26). New World ..... *Eumicrota* Casey, p. 249
- 12' Setal patch on tergum 10 more or less square (Figures 162–164). Prothorax of most specimens 1.2 to 1.7 times as wide as long. Body of most specimens slightly pubescent to subglabrous. Antenna short or elongate, with antennomeres 4 to 10 slightly transverse to elongate or various in same specimen ..... 13
- 13 (12') Eyes extremely large, occupying most of lateral margins of head (Figures 12, 13). World-wide ..... *Phanerota* Casey, p. 246
- 13' Eyes moderate in size (Figures 7–11). World-wide ..... *Gyrophaena* Mannerheim, p. 242

## GENERA AND SUBGENERA OF GYROPHAENINA

### *Gyrophaena* Mannerheim

Figs. 7-11, 21-24, 29-32, 56, 73, 74, 98, 99, 119-122, 131, 137, 142, 143, 149, 156, 162, 163, 176-178, 192-194, 216, 217, 233, 234, 240, 241, 245, 246

*Gyrophaena* Mannerheim 1830:488. Type species: *Gyrophaena nana* (Paykull) (from *Staphylinus*). Fixed by Westwood 1838:20 by subsequent designation. —Mannerheim 1830:488. —Erichson 1837:365. —Erichson 1839-40:182. —Lacordaire 1854:43. —Kraatz 1856:352. —Jacquelin du Val 1857-59:18. —Thomson 1860:266. —Mulsant and Rey 1871:17. —Fauvel 1875:631. —Fowler 1888:183. —Ganglbauer 1895:297. —Casey 1906:278. —Reitter 1909:83. —Blatchley 1910:340. —Fenyès 1918-21:95. —Cameron 1922:638. —Scheerpeltz 1930:70. —Wüsthoff 1937:137. —Cameron 1939:56. —Scheerpeltz and Höfler 1948:163. —SeEVERS 1951:673. —Likovsky 1964:52. —Batten 1973:63. —Lohse 1974:21. —SeEVERS 1978:161.

**Diagnostic combination.**— Ligula entire, produced as more or less parallel-sided lobe. Eyes moderate in size. Hypomera slightly to broadly visible in lateral aspect. Mesosternum without medial longitudinal carina. Setal patch on tergum 10 more or less square, setae flattened. In addition, most members of *Gyrophaena* are distinguished by the subglabrous body; broadly oval or subquadrate pronotum (1.3 to 1.6 times as wide as long); more or less transverse head (1.1 to 1.3 times as wide as long); and prosternum with slight transverse carina and without medial knob, carina or protuberance.

**Description.**— Length 1.0 to 3.0 mm. Body parallel-sided, slightly flattened (in most specimens) to slightly robust. Sculpture reticulate, obsoletely reticulate or smooth, but uniform throughout or various on different regions of body. Surface subshining to shining in most species, dull in some; moderately to slightly pubescent, subglabrous, or glabrous, individuals of most species slightly pubescent to subglabrous.

**Head.** (Figures 7–11) — More or less transverse in most species, subquadrate to elongate in some; head held more or less in plane of body; sculpture various; microsetae numerous, short and stiff, to fewer, longer and more widely scattered; punctures small to large, asperite in specimens of some species; pair of darker macrosetae medially on vertex of head in specimens of a very few species (Figure 10), absent from most. Eyes moderate in size. Infraorbital carina moderately to markedly developed. Neck carina well developed. Antennae very variable within genus; antennomere 4 similar to 1-3.

**Mouthparts.** Labrum (Figures 29–32) with major setae distinct, additional setae absent; sensilla of medial sensory area distinct; lateral sensilla row distant from lateral margin. Maxilla (Figures 73, 74, 233, 234) with tip of lacinia truncate with well developed "spore brush"; number and size of teeth various; relatively few, large, widely spaced teeth (Figure 233) to moderately numerous, smaller, more closely spaced teeth; internal face of lacinia with single row of many to few, large setae, and three or four widely spaced hyaline sensilla; galea with apical setae in four distinct rows, setae subspatulate to plate-like. Mandibles (Figure 56) not bifid at tip; right mandible with small to large internal tooth. Prostheca typical of subtribe. Labium (Figures 98, 99) with ligula undivided, entire, produced as a more or less parallel-sided lobe; medial seta one or, in specimens of a few species, absent.

**Thorax.** Prothorax transverse, broadly oval to subquadrate; specimens of most species with slightly transverse, broadly oval pronota, 1.6 to 1.3 times as wide as long (Figures 119–122); flat, slightly convex or moderately convex in cross section, sides not, slightly, or, in some species, moderately depressed; antero-lateral borders not markedly depressed; hypomera not, partially, or fully visible in lateral aspect; anterior margin straight or broadly rounded; posterior margin slightly to, in most specimens, not at all bisinuate, hind margin of some species with a slight to moderate medial emargination; sculpture reticulate, obsoletely reticulate, or smooth, integument subshining to markedly shining; microsetae various— numerous, more or less densely and uniformly distributed (surface pubescent), to very few and widely scattered (surface subglabrous to glabrous); punctures small to large, asperite or not; macrosetae small and inconspicuous to large and conspicuous; arrangement typical of subtribe; punctures of macrosetae in medial row of many large, conspicuous. Elytra shorter than, equal to or longer than pronotum; outer apical angles slightly to not at all sinuate (Figure 131); integument reticulate to smooth, subshining to markedly shining; microsetae numerous to few, uniformly distributed, punctures small to large, asperite in many species; macrosetae inconspicuous to conspicuous; prosternum transverse to slightly transverse; specimens of most species with slight transverse raised ridge or carina (Figures 142, 143), or transverse carina absent; without prominent medial knob, carina or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process varied in length, extended from slightly beyond middle of mesocoxal cavities to posterior margin of coxal cavities. Metasternal process truncate or broadly rounded; isthmus absent. Suture between meso- and metasternal process fused in some species, distinct in most. Coxae widely separated. Setae on metepisternum numerous to few, in single row, setose area more or less delimited ventrally by fine carina or not (Figures 156, 245, 246). Tarsomere 1 of hind legs various: equal in length to second tarsomere to as long as next two combined (slightly longer in a few species); tarsomere 1 of hind leg with a slightly to markedly developed ctenidium on inner ventral surface.

*Abdomen.* Flattened to slightly robust; sides parallel. Terga 3-5, 3-6 or 3-7 markedly to slightly transversely impressed. Sterna 3-5 very slightly transversely impressed to unmodified. Tergum 7 with anterior border modified as openings for abdominal gland ducts. Tergum 10 with setal patch more or less square; setae numerous to few, flattened, subspatulate to spatulate.

*Aedeagus.* (Figures 192-194) — Extremely varied among species. Median lobe with apical process simple to strikingly modified and complex, asymmetrical in many; flagellum tubular, whip-like or very complex. Parameres (Figures 216, 217) simple to complex and asymmetrical.

*Spermatheca.* Typical of subtribe; simple (Figures 176, 178) or with slightly elongate neck (Figure 177).

*Secondary sexual characteristics.* Very varied. Males of most species with posterior margin of tergum 8 broadly or narrowly incised, incision with more or less well developed spines on each side, with or without one or more teeth or spines medially within incision. Many males with tergum 7 with carinae, spines or knobs. Other terga modified or not. Some males with spines, carinae or asperities on elytra. Males of some with sternum 8 emarginate medially. Some males with tergum 10, fewer with tergum 9 or sternum 10, modified. Females of some species with integumental modifications; if so, males and females of same species with markedly to slightly different modifications.

*Discussion.*— *Gyrophaeina* as presently recognized is the most heterogeneous genus among gyrophaeines. Typically, members have been recognized by presence of widely separated coxae, exposed hypomera and moderately sized eyes (Seevers, 1951), or these in addition to a transverse head and shining subglabrous integument (Lohse, 1974). This combination is inadequate for recognition of all species that should be placed in this genus, resulting in confusion about limits of the genus as indicated by, among other things, the question of whether or not *Agaricochara* Kraatz should be considered a subgenus of *Gyrophaeina*. The characters provided in the diagnostic combination should help clarify assignments to this genus.

No derived character state is shared among all members of *Gyrophaeina*. Therefore, as presently conceived, *Gyrophaeina* cannot be shown to represent a monophyletic assemblage. It is, instead, paraphyletic in relation to *Phanerota* (see Phylogenetic Analysis). This appears to result from the great heterogeneity of forms now included within *Gyrophaeina*. It seems likely that *Gyrophaeina* could be divided into several genus-level monophyletic groups. This, however, would require detailed study of the world *Gyrophaeina*, a monumental task.

Within *Gyrophaeina*, a number of monophyletic groups are recognized. General form of the median lobe of the aedeagus and structure of secondary sexual modifications are most useful for recognition of monophyletic groups, but antennal structure, sculpture, pubescence and general body dimensions may be useful in combination with aedeagal structures. Seevers (1951) used primarily aedeagal structure in forming his "species groups", most of which were probably monophyletic.

*Natural history.*— Most members of *Gyrophaeina* are found on fleshy gilled mushrooms as both larvae and adults. Some are more common on fleshy polypores (see Table 4). Donisthorpe (1935), Scheerpeltz and Höfler (1948) and Benick (1952) give host mushroom lists for European *Gyrophaeina*. White (1977) has studied general characteristics of host mushrooms of members of *Gyrophaeina*. Few details of life history and habits of individual species are available.

*Immature stages.*— Few detailed studies of immature stages are available. Larvae of *G. affinis* Sahlberg (Rey, 1886), *G. cristophera* Cameron (Paulian, 1941), *Gyrophaeina* sp. (Böving and Craighead, 1930), *G. gentilis* Erichson (White, 1977) and *G. strictula* Erichson (White, 1977) have been described. Of these, only White (1977) and Paulian (1941) provide detailed descriptions and illustrations. Larvae described as those of *G. manca* Erichson by Haeger (1853) are not *Gyrophaeina* (see White, 1977).

*Distribution.*— Members of the genus *Gyrophaeina* occur throughout the world, except, as far as is known, in alpine and tundra areas.

*Major literature.*— Few papers about *Gyrophaeina* include keys or illustrations, and descriptions are inadequate. The European fauna is best known. Keys and descriptions of

European *Gyrophæna* are provided by a number of faunal studies including: Scheerpeltz and Höfler (1948) (areas around Vienna, Austria), Lohse (1974) (middle Europe), Seevers (1951) (with North American fauna), Wüsthoff (1937) (European fauna), Likovsky (1964) (Czechoslovakian fauna), and White (1977) (British fauna). Seevers (1951) provides keys, descriptions and illustrations of North American species. Cameron (1939) provides keys and descriptions of the known Indian species. No other comprehensive faunal studies of *Gyrophæna* with adequate keys and descriptions are available.

### Review of the Subgenera of *Gyrophæna* Mannerheim

Genera and subgenera associated with the name *Gyrophæna* are a complex of inadequately defined and arbitrarily arranged groups, as indicated by the various treatments of them summarized here. Casey (1906, 1911) recognized four genera within his subtribe Gyrophænae: *Phanerota* Casey, *Phænogyra* Mulsant and Rey, *Eumicrota* Casey and *Gyrophæna* Mannerheim. Fenyès (1918-21) assigned subgeneric rank to *Phanerota*, *Phænogyra* and *Eumicrota*. However, he recognized that *Phanerota* may warrant consideration as a genus. He retained the genus *Agaricochara* Kraatz for several species that occur in Europe and America, separating it from *Gyrophæna* by the bifid ligula, wider pronotum and less conspicuous eyes of the former.

Scheerpeltz and Höfler (1948) recognized three subgenera of European *Gyrophæna*: *Gyrophæna s. str.*, *Phænogyra* and *Leptarthrophæna* Scheerpeltz and Höfler. Within *Phænogyra* were placed those species in which the head of adults was relatively long in relation to interocular width. They established the subgenus *Leptarthrophæna* to include those species in which adults have antennomeres 5-10 distinctly elongate. In addition, they retained the genus *Agaricophæna* Reitter for *A. boleti* (L.).

Seevers (1951) eliminated the subgenus *Phænogyra* and assigned the species to species group status, claiming that it was no more deserving of subgeneric status than most other species groups within *Gyrophæna s. st.* In addition, he showed that *Leptarthrophæna* was a conglomerate of several unrelated species, and that *Gyrophæna* could not be divided into subgenera solely on the basis of antennal structure of adults. Seevers followed Fenyès (1918-21) in recognizing *Eumicrota* Casey as a subgenus, but reduced *Agaricochara* Kraatz to subgeneric status within *Gyrophæna*. He separated adults of *Eumicrota* and *Agaricochara* on the basis of adult antennal character states (in spite of his previous statement that this was impossible). He believed that they are closely related and may be combined into a single genus when more is known about the Neotropical forms. He was unable to separate *Agaricophæna* and placed it in synonymy with *Agaricochara*. Finally, Seevers reassigned generic rank to *Phanerota* although he did not give reasons for doing so. He also recognized that the subgenus *Acanthophæna* Cameron was consubgeneric with *Phanerota*. Seevers (1978) raised *Eumicrota* and *Agaricochara* to generic rank.

At one time or another 11 subgenera (including *Gyrophæna s. st.*) have been assigned to *Gyrophæna* Mannerheim. In this revision three are given generic rank: *Agaricochara* Kraatz, *Eumicrota* Casey and *Phanerota* Casey; *Acanthophæna* Cameron is placed as a subgenus of *Phanerota* and *Leptarthrophæna* is shown to be indefinable (as pointed out by Seevers (1951)). Additionally, *Allocota* Bernhauer is not a member of the Gyrophænina.

For reasons given above, this key does not include the following taxa: *Agaricochara* Kraatz, *Eumicrota* Casey, *Phanerota* Casey, *Leptarthrophaena* Scheerpeltz and Höfler, *Acanthophaena* Cameron, and *Allocota* Bernhauer. Taxa included are not necessarily monophyletic, nor is the key likely to assign members of all species to useful groups when the world fauna is considered.

- |        |   |       |   |
|--------|---|-------|---|
| 1      | Abdomen of male with lateral margins of sterna 3 and 4 produced as spines or appendiculate processes  | ..... | <i>Enkentrophaena</i> Eichelbaum, p. 246  |
| 1'     | Abdomen of male without lateral margins of sterna 3 and 4 produced as spines or processes   | ..... | 2   |
| 2 (1') | Head transverse (1.2 to 1.4 times as wide as long), moderately and obliquely narrowed behind the eyes. Specimens of most species slightly pubescent to subglabrous                                | ..... | 3   |
| 2'     | Head slightly transverse to longer than wide (1.1 to 0.8 times as wide as long); slightly and gradually narrowed behind eyes. Specimens of most species moderately pubescent                      | ..... | 4   |
| 3 (2)  | Large (adults 3.0 to 3.5 mm in length); very robust Terga 3 and, in some, 4, of males with median keel. Antennomere 4 longer than broad.  | ..... | <i>Orphnebioidea</i> Schubert, p. 246     |
| 3'     | Smaller (adults 1.0 to 3.0 mm in length); less robust, most more or less flattened and parallel-sided. Terga 3 and 4 of males without median keel. Most with antennomere 4 quadrate or transverse | ..... | <i>Gyrophaena s. st.</i> , p. 245         |
| 4 (2') | Larger (adults 1.3 to 2.1 mm in length). Head 1.2 to 0.7 times as wide as long. Pronotum 1.5 to 1.1 times as wide as long   | ..... | <i>Phaenogyra</i> Mulsant and Rey, p. 245 |
| 4'     | Smaller (adults 0.9 to 1.2 mm in length). Head 1.2 times as wide as long. Pronotum 1.5 times as wide as long  | ..... | <i>Agaricophaena</i> Reitter, p. 246      |

*Gyrophæna* s. str.

*Gyrophæna* Mannerheim 1830:488. Type species: *Gyrophæna nana* (Paykull). —Ganglbauer 1895:300. —Fenyès 1918-21:97. —Cameron 1939:65. —Scheerpeltz and Höfler 1948:163. —SeEVERS 1951:673. Lohse 1974:27.

*Agaricochara* Kraatz

*Agaricochara* Kraatz 1856:361. Type species: *Agaricochara laevis* Kraatz. Fixed by Kraatz 1856:361 by monotypy.  
—Kraatz 1856:361 (genus). —Mulsant and Rey 1871:90 (genus). —Ganglbauer 1895:304 (genus). —Casey 1906:278 (genus). —Reitter 1909:85 (genus). —Fenyés 1918-21:92 (genus). —Scheerpeltz 1930:70 (genus). —SeEVERS 1951:740 (subgenus of *Gyrophana*). —Lohse 1974:130 (genus). —White 1977:304 (subgenus of *Gyrophana*). —SeEVERS 1978:163 (genus).

*Notes:* Treated as a genus in this revision.

*Phaenogyra* Mulsant and Rey

*Phaenogyra* Mulsant and Rey 1872:166. Type species: *Phaenogyra strictula* (Erichson) (from *Gyrophaena*). Fixed by Fenyés 1918-21:24 by subsequent designation. —Mulsant and Rey 1871:76 (genus). —Casey 1906:278 (genus). —Reitter 1909:85 (subgenus of *Gyrophaena*). —Fenyés 1918-21:101 (subgenus of *Gyrophaena*). —Cameron 1939:140 (subgenus of *Gyrophaena*). —Scheerpeltz and Höfler 1948:177 (genus). —SeEVERS 1951:724 (*G. strictula* species group of *Gyrophaena*). —White 1977:304 (within subgenus *Agaricochara*).

*Eumicrota* Casey

*Eumicrota* Casey 1906:280. Type species: *Eumicrota corruscula* (Erichson) (from *Gyrophæna*). Fixed by Fenyès

1918-21:22 by subsequent designation. —Casey 1906:280 (genus). —Fenyès 1918-21:101 (subgenus of *Gyrophaena*). —SeEVERS 1951:732 (subgenus of *Gyrophaena*). SeEVERS 1978:162 (genus).

**Notes:** Treated as a genus in this revision.

### *Phanerota* Casey

*Phanerota* Casey 1906:285. Type species: *Phanerota fasciata* (Say) (from *Gyrophaena*). Fixed by Blackwelder 1952:299 by subsequent designation. —Casey 1906:285 (genus). —Fenyès 1918-21:96 (subgenus of *Gyrophaena*). —SeEVERS 1951:747 (genus). —SeEVERS 1978:162 (genus).

### *Orphnebioidea* Schubert

*Orphnebioidea* Schubert 1908:611. Type species: *Orphnebioidea rosti* (Schubert) (from *Gyrophaena*). Fixed by Schubert 1908:611 by monotypy. —Schubert 1908:611 (subgenus). —Fenyès 1918-21:97 (subgenus). —Cameron 1939:61 (subgenus).

### *Agaricophaena* Reitter

*Agaricophaena* Reitter 1908:85. Type species: *Agaricophaena boleti* (Linnaeus) (from *Staphylinus*). Fixed by Reitter 1909:85 by original designation. —Reitter 1909:85 (subgenus of *Gyrophaena*). —Fenyès 1918-21:102 (subgenus of *Gyrophaena*). —Scheerpeltz and Höfler 1948:163 (genus). —SeEVERS 1951:740 (within subgenus *Agaricochara*). —Likovsky 1964:53 (within subgenus *Agaricochara*). —White 1977:311 (within subgenus *Agaricochara*).

### *Enkentrophaena* Eichelbaum

*Enkentrophaena* Eichelbaum 1913:139. Type species: *Enkentrophaena plicata* (Fauvel) (from *Gyrophaena*). Fixed by Blackwelder 1952:149 by subsequent designation. —Eichelbaum 1913:139 (subgenus of *Gyrophaena*). —Fenyès 1918-21:96 (subgenus of *Gyrophaena*). —Cameron 1939:57 (subgenus of *Gyrophaena*).

### *Acanthophaena* Cameron

*Acanthophaena* Cameron 1934:23. Type species: *Acanthophaena appendiculata* (Motschulsky) (from *Gyrophaena*). Fixed by Blackwelder 1952:34 by subsequent designation. —Cameron 1934:23 (subgenus of *Gyrophaena*). —Cameron 1939:59 (subgenus of *Gyrophaena*).

**Notes:** Treated as a subgenus of *Phanerota* Casey in this revision.

### *Leptarthrophaena* Scheerpeltz and Höfler

*Leptarthrophaena* Scheerpeltz and Höfler 1948:64. Type species: *Leptarthrophaena affinis* (Sahlberg) (from *Gyrophaena*). Fixed by Blackwelder 1952:215 by subsequent designation. —Scheerpeltz and Höfler 1948:64 (subgenus of *Gyrophaena*). —SeEVERS 1951:670-671 (shown to be untenable subgenus).

### *Allocota* Bernhauer

*Allocota* Bernhauer 1916:428. Type species: *Allocota abnormalis* Bernhauer. Fixed by Bernhauer 1916:428 by monotypy. —Bernhauer 1916:428 (subgenus of *Gyrophaena*).

**Notes:** According to Blackwelder (1952), *Allocota* Bernhauer is a junior homonym of *Allocota* Motschulsky 1860 and a synonym of *Razia* Bernhauer (renamed by Blackwelder 1952:82). Blackwelder (1952:46) transferred this taxon to *Bolitochara* Mannerheim as a subgenus. However, examination of Motschulsky (1860) did not confirm a previous citation of *Allocota*. In addition, Bernhauer and Scheerpeltz (1926) did not recognize a citation of *Allocota* Motschulsky 1860 and placed *Allocota* Bernhauer as a subgenus of *Astilbus* Dillwyn.

### *Phanerota* Casey

Figs. 12, 13, 25, 33, 34, 58, 75, 76, 100, 101, 123, 132, 144, 151, 161, 164, 165, 179, 180, 195, 196, 218

*Phanerota* Casey 1906:285. Type species: *Phanerota fasciata* (Say) (from *Gyrophaena*). Fixed by Blackwelder 1952:299 by subsequent designation. —Casey 1906:285. Fenyès 1918-21:96. —Cameron 1934:23. —Cameron 1939:59. —SeEVERS 1951:747. —SeEVERS 1978:162

**Diagnostic combination.**—Eyes extremely large, extended almost entire length of lateral margins of head. Ligula entire, protruded, more or less parallel-sided. Microsetae sparse, integument subglabrous. Spermatheca with neck elongate and coiled proximal to plate-like flange. Aedeagus form distinctive (Figures 195, 196).

**Description.**—Length approximately 1.5 to 3.0 mm. Body more or less flattened, parallel-sided. Sculpture reticulate, obsoletely reticulate, or smooth, uniform throughout body or various on different sclerites, surface subshining to markedly shining. Body slightly pubescent to subglabrous; microsetae few, small and scattered in specimens of most species; punctures moderate to small, asperite or not. Macrosetae moderately large and conspicuous or rather small and

inconspicuous.

**Head** (Figures 13, 14). More or less transverse, held more or less in plane of body; sculpture various; microsetae various, specimens of most species with few to very few widely scattered microsetae; punctures moderate to very fine; macrosetae two pairs, one medial to each of anterior and posterior margins of eye, or absent. Eyes very large, globose, extended most of length of lateral margin of head, tempora obsolete; eyes coarsely faceted. Infraorbital carina markedly to very markedly developed, complete ventrally as medio-ventral margin of eyes, or obsolete anteriorly. Neck carina markedly developed. Antenna various, typical of subtribe; antennomere 4 similar to 1-3; antennomere 4 subquadrate to elongate; 5-10 elongate, subquadrate or slightly transverse (Figure 25).

**Mouthparts.** Labrum (Figures 33, 34) with major setae distinct, additional setae absent; sensilla of medial sensory area well developed; lateral sensilla row distant from lateral margin. Maxilla (Figures 75, 76) with tip of lacinia with well developed "spore brush"; teeth relatively large, close to moderately spaced; internal face of lacinia with moderate to many large to medium sized setae and two or three widely spaced hyaline setiform sensilla; galea with apical setae in four distinct rows, setae flattened, subspatulate to plate-like. Mandible (Figures 57, 58) rather robust, not bifid at tip; right mandible with large internal tooth. Prostheca typical of subtribe. Labium (Figures 100, 101) with ligula entire, produced as a more or less parallel-sided lobe, sides slightly convergent from base to more or less broad apex in specimens of some species; apical half of ligula inclined ventrally in specimens of some species; medial seta 1, reduced or absent in specimens of many species.

**Thorax** (Figure 123). Pronotum slightly transverse, broadly oval in outline, approximately 1.3-1.6 times as wide as long; flat or slightly convex in cross section, sides not or slightly depressed; antero-lateral border not markedly depressed; hypomera partially to fully visible in lateral view; anterior margin straight or broadly rounded; hind margin not bisinuate, not medially emarginate; sculpture reticulate, obsolete reticulate or smooth, integument subshining to markedly shining; microsetae small, few to very few, widely scattered; punctures fine to moderate; macrosetae moderately large, conspicuous to small, inconspicuous; arrangement typical of subtribe. Elytra (Figure 132) equal to or slightly longer than pronotal length; outer apical angles very slightly to not at all sinuate; sculpture reticulate to smooth; microsetae few, widely scattered; punctures medium to fine, asperate or not; macrosetae moderately large to small. Prosternum (Figure 144) transverse to slightly transverse; with or without fine transverse carina, or carina obsolete medially; without medial spine, carina or protuberance. Mesosternum without medial longitudinal carina; mesosternal process extended to middle or slightly posterior to middle of midcoxae cavities (Figure 151). Metasternal process extended anteriorly in broad contact with mesosternal process, suture unmodified, not fused; isthmus absent; apex of metasternal process truncate or broadly rounded. Coxae widely separated. Metepisternal setae numerous to few, in single row; setose area delimited antero-laterally by fine carina or not. Hind tarsus (Figure 161) with first tarsomere as long as next two together, or, in specimens of some species, 1.0 to 1.5 times length of tarsomere 2; with well developed ctenidium on ventral surface.

**Abdomen.** More or less flattened. Sides parallel. Terga 3-5 or 3-6 markedly to moderately transversely impressed. Sterna unmodified. Tergum 7 with anterior border modified as opening for abdominal gland ducts. Tergum 10 (Figures 164, 165) with medial setal patch more or less square, setae numerous to few, flattened, subspatulate.

**Aedeagus.** (Figures 195, 196, 218). Known species with apical lobe of median lobe long, slender, and spine-like. Flagellum long, slender, more or less whip-like. Parameres not exceptionally modified (Figure 218).

**Spermatheca.** Neck elongate, coiled and/or convoluted proximal to plate-like flange (Figures 179, 180).

**Secondary sexual characteristics.** Both males and females with tergum 8 shallowly to deeply emarginate medially. Females with middle of emargination unmodified or with very broad low lobe internally. Males with emargination with more or less distinct lobe internally. Males of some species with carina near postero-lateral margin of elytra. Males of some species with lateral margins of sternite 5 modified as leaf-like lobe and/or lateral paratergite 5 with thick spine. Males of some species may also have some tergites or paratergites broadened and flattened and/or transverse impressions of tergites deepened.

**Discussion.**— Casey (1906) described *Phanerota* to include several North American, West Indian and Mexican species. Fenyés (1918-21) ranked *Phanerota* as a subgenus of *Gyrophaena*, although he recognized that *Phanerota* may warrant generic status because he believed that the very large eyes crowd out the infraorbital carina. Seevers (1951) recognized *Phanerota* as a genus based primarily on the large eyes, lack of an infraorbital carina, and distinctive spermatheca. Both Seevers and Fenyés were incorrect since the infraorbital carinae are indeed present, although the large eyes encroach upon them so that the carinae form the medio-ventral margins of the orbit.

Seevers (1951) recognized that *Acanthophaena* Cameron was congeneric with *Phanerota*, but he did not formally place the names in synonymy. Based on the shared characteristics of extremely large eyes, similar secondary sexual characteristics, particularly those on tergum 8, similar spermatheca, and similar median lobe of the aedeagus, it seems appropriate to consider *Phanerota* Casey and *Acanthophaena* Cameron to represent a single genus.





tergum 8 similar to that of *Phanerota s. st.* Tergum 7 with or without carinae near apico-lateral margins. Sterna with or without some lateral margins thickened; sternum 5 with each lateral margin with well developed, posteriorly directed lamelliform process; lateral paratergum 5 broadened and with large posteriorly directed spine or not. Terga and paraterga 3-5 or 3-6 markedly broadened, flattened, and transverse impressions deepened.

### *Eumicrota* Casey

Figs. 14, 26, 35, 59, 77, 102, 124, 125, 133, 139, 145, 166, 181, 197, 198, 219, 235, 247

*Eumicrota* Casey 1906:280. Type species: *Eumicrota corruscata* (Erichson) (from *Gyrophaena*). Fixed by Fenyes 1918-21:22 by subsequent designation. —Casey 1906:280. —Fenyes 1918-21:101. —Seevers 1951:732. —Seevers 1978:162.

**Diagnostic combination.**— Size small (most adults 1.0 mm or less in length). Pronotum transverse, 1.7-2.1 times as wide as long. Ligula entire, protruded, more or less parallel-sided. Tergum 10 with setal patch in distinct V-shaped row. Aedeagus form distinctive (Figure 197).

**Description.**— Minute to very small, length approximately 0.6 to 1.5 mm, adults of most species 1.0 mm or less in total length. Body of most dark, piceous, brownish-black or black. Body parallel-sided, flattened to slightly robust. Body sculpture reticulate throughout in most; integument shining to subshining; moderately to more or less markedly pubescent, setae short, numerous and uniformly and closely spaced in most species, setae fewer and less densely arranged in some. Punctures moderate to small, asperate in many.

**Head** (Figure 14). More or less transverse; held more or less in plane of body to slightly deflexed; sculpture reticulate; microsetae short, numerous and densely arranged in most, or fewer and more sparsely arranged; punctures fine to minute. Macrosetae absent in specimens of most species, some with very small, difficult to distinguish, pair of macrosetae medially on vertex. Eyes moderate in size. Infraorbital carina complete, moderately to markedly developed. Neck carina distinct. Antenna (Figure 26) short, in majority of species not longer than head and pronotum together; antennomere 4 similar to 1-3; specimens of most species with antennomere 4 small, transverse to subquadrate; 5 wider than 4; 6-10 markedly transverse, subequal to 5 in width so that antennomeres 5-10 form a loose, parallel-sided club; specimens of some species with antenna more elongate, article 4 longer than wide, 5 quadrate, and 6-10 transverse (see discussion below).

**Mouthparts.** Labrum (Figure 35) with major setae distinct, additional setae absent; medial sensory area with sensilla well developed; lateral sensory row present, distant from lateral margin, three or four sensilla. Mandibles (Figure 59) typical of subtribe. Not bifid at apex; right mandible with small tooth internally, or tooth very slightly developed. Maxilla (Figures 77, 235) with apex of lacinia truncate, with well developed "spore brush"; teeth of spore brush small, numerous and densely arranged in most; internal face of lacinia with three or four large, hyaline setiform sensilla; galea with apical setae in four distinct rows, setae subspatulate to plate-like. Labium (Figure 102) with ligula entire, produced as a more or less parallel-sided lobe; single medial seta.

**Thorax.** Pronotum (Figures 124, 125) markedly transverse, 1.7 to 2.1 times as wide as long; slightly to moderately convex in cross section, sides slightly to moderately depressed, antero-lateral borders moderately depressed; hypomera narrowly visible to not visible in lateral view; anterior margin of pronotum straight. Posterior margin moderately, very slightly, or in specimens of a few species, not at all bisinuate; posterior margin not emarginate medially; pronotal sculpture reticulate; integument subshining or dull; microsetae various, short, numerous, and uniformly distributed in most species to fewer and sparsely distributed; punctures sparse and fine to slightly asperate; macrosetae small, inconspicuous, difficult to distinguish from microsetae in most. Elytra (Figure 133) equal to or longer than pronotal length; outer apical angles moderately to very slightly sinuate; integument reticulate, subshining to dull; microsetae numerous, uniformly distributed in most species, asperately punctate or not; macrosetae inconspicuous, as in *Gyrophaena*. Prosternum (Figure 145) transverse to strongly transverse; with or without faint transverse carina; without prominent medial knob, carina or protuberance. Mesosternum without medial longitudinal carina; mesosternal process length various, extended from slightly beyond middle to posterior 1/4 of middle coxal cavities; juncture with metasternal process broadly truncate, suture fused in specimens of a few species; isthmus absent. Coxae widely separated. Setae on metepisternum numerous to few, in single row; setose area not delimited by a carina or with very slight carina anteriorly. Tarsomere 1 of hind tarsus equal in length or slightly longer than 2, with indistinct ctenidium on inner surface.

**Abdomen.** Flattened, sides parallel. Terga 3-5 (6 very slightly in some) moderately to slightly transversely impressed. Sterna unmodified. Tergum 7 with anterior border modified for opening of abdominal gland ducts. Tergum 10 (Figure 166) with medial setal patch arranged in distinct V-shaped rows; setae unmodified or flattened.

**Aedeagus.** (Figures 197, 198, 219) — Most species in genus with variation on very distinctive basic form. Median lobe with apical process slender and elongate; in most with knob or hook-like structure apically. Flagellum elongate, whip-like, and apical half looped or more tightly coiled. Parameres not extensively modified (Figure 219).

**Spermatheca** (Figure 181). Typical of subtribe, simple.

*Secondary sexual characteristics.* Varied among species. Posterior margin of tergum 8 of male (and in some species, female) of many species broadly emarginate. Males of others with posterior margin of tergum 8 lobed or toothed medially. Other terga modified or not. Males of some species with lateral margins of sterna modified. Some tropical species with male and female with distinctively different sexual modifications.

*Discussion.*— Seevers (1951, 1978) believed that *Eumicrota* Casey was closely related to *Agaricochara* Kraatz, and the two genera should possibly be combined. He based this primarily on similarities in the very transverse pronotum and similar intercoxal processes. It appears, however, that *Eumicrota* and *Agaricochara* are not closely related within the Gyrophaenina (see Phylogenetic Analysis). *Eumicrota* is a very distinct group, and, based on the derived characters of general form of the median lobe of the aedeagus and the V-shaped setal patch on tergum 10, it is almost certainly monophyletic.

Most members of *Eumicrota* have a characteristic habitus of small size, dark color, transverse pronota, and very transverse antennomeres. However, a few Neotropical gyrophaenines share the derived character states of *Eumicrota* (aedeagal form, and form of setal patch on tergum 10), but are larger and have a general habitus more similar to that of members of *Gyrophaena* s. st., and elongate antennomeres. *Gyrophaena varians* Sharp also has male and female specimens with markedly different secondary sexual characteristics. Because they share derived characters with other *Eumicrota*, these are here considered to belong to this genus.

*Natural history.*— As far as is known, members of *Eumicrota* are found most commonly on fleshy polypore mushrooms on logs. They can also be found in large numbers on some more persistent gilled mushrooms on logs, and on woody and/or resupinate polypore mushrooms (Seevers, 1951, and personal observations).

*Immature stages.*— Immature stages of members of *Eumicrota* have not been described.

*Distribution.*— As far as is presently known, members of *Eumicrota* are limited to the New World. Most species are tropical or subtropical. Seven species occur in America north of Mexico. Two of these are widespread in eastern North America. Others are limited to the Gulf States or Southwest. Several described West Indian and Central American species should be assigned to this genus, and I have seen many undescribed species from Mexico, Central America and South America.

*Major literature.*— Only Casey (1906) and Seevers (1951) provide more or less useful keys and descriptions of members of *Eumicrota*. Both of these are North American in scope.

### *Encephalus* Kirby

Figs. 36, 60, 61, 78-80, 103, 104, 134, 157, 167, 182, 183, 199, 200, 201, 220, 221

*Encephalus* Kirby 1832:163. Type species: *Encephalus complicans* Kirby (in Stephens 1832:163). Fixed by Stephens 1832:163 by monotypy. —Kirby 1832:163. —Kraatz 1856:351. —Thomson 1860:265. —Mulsant and Rey 1871:11. —Fauvel 1875:630. —Fowler 1888:151. —Ganglbauer 1895:304. —Casey 1906:279-280. —Reitter 1909:85. —Fenyès 1918-21:94. —Scheerpeltz 1930:70. —Seevers 1951:752. —Lohse 1974:26. —Seevers 1978:163.

*Diagnostic combination.*— (Holarctic species only) Very robust, broadly oval in dorsal aspect. Head markedly deflexed into vertical plane. Antenna short, as long as head and pronotum together; antennomeres 5-10 transverse, 6-10 in form of a loose incrassate club. Pronotum markedly convex, hypomera not visible in lateral aspect. Ligula broadly rounded. Mesothorax in vertical plane. Mesosternal process very wide and long, extended to posterior margin of middle coxal cavities. Middle coxae very widely separated.

*Description.*— Length approximately 1.5 to 2.2 mm. Body shape broadly oval, robust, oval in cross section. Body sculpture markedly reticulate throughout; body subshining. Body subglabrous, setae few, short, widely scattered; punctures small.

**Head.** Slightly transverse, much narrower than anterior margin of prothorax; inclined, oblique to almost vertical; reticulate throughout; microsetae small, few, widely scattered; punctures very small to moderate; macrosetae absent. Eyes moderate in size. Infraorbital carina complete, well developed. Neck carina well developed. Antenna short, about as long as head and pronotum together; antennomere 4 similar to 1-3; antennomeres 5-10 transverse; 6-10 gradually increased in width distally, in form of loose incrassate club.

**Mouthparts.** Labrum (Figure 36) with major setae distinct, without accessory setae; lateral sensilla row slightly developed or absent; medial sensory area with sensilla well developed or reduced. Mandibles (Figure 60) not bifid at apex, right mandible with small internal tooth. Prostheca typical of subtribe. Maxilla (Figures 78, 79) with tip of lacinia truncate with well developed spore brush; spines relatively thick and long, widely spaced. Setae on inner face of lacinia in single row; inner face of lacinia with three or four widely spaced hyaline sensilla; galea with apical setae in four distinct rows, setae subspatulate to plate-like. Labium (Figure 103) with ligula entire, produced as broadly rounded lobe; single medial seta.

**Thorax.** Pronotum moderately to markedly transverse, 1.7 to 2.0 times as wide as long, markedly convex; sides moderately depressed, in dorsal aspect narrowed and broadly rounded proximal to apical angles, these acute, very markedly depressed, embracing sides of head; hypomera not visible in lateral aspect; anterior margin straight or broadly emarginate and bisinuate, covering base of head; hind margin broadly rounded, not bisinuate, with medial emargination; sculpture reticulate throughout; microsetae few, slight, scattered, punctures small; macrosetae small, M.L.2 and M.L.4 very reduced, small or absent; punctures small. Each elytron wider than long; sutural length less than or subequal to pronotal length; outer apical angles rounded, not sinuate; apical and sutural margin depressed and narrowly beaded; surface uniformly reticulate throughout; microsetae few to moderate in number, punctures very small to small. Prosternum slightly to moderately transverse with a slight transverse ridge; without prominent medial knob, carina or protuberance; markedly declivous posteriorly. Mesosternum markedly declivous with slight medial longitudinal carina, indistinct before apex of process or not carinate but with very slight, low, medial ridge in anterior 2/3; mesosternal process very wide, extended to posterior margin of middle coxal cavities, apex truncate or broadly rounded. Metasternal process not extended between coxal cavities; suture between processes complete, not fused, slightly raised as low bead; isthmus absent. Metepisternum (Figure 157) with few setae in single row on posterior 1/3; setose area delimited by faint carina anteriorly. Tarsomere 1 of hind tarsus about as long as 2, with six or seven setae in form of slight ventro-lateral ctenidium.

**Abdomen.** Broadly oval in dorsal aspect, robust. Terga markedly transverse, together in form of broad flat plane. Terga 3-5 (or 3-6) slightly transversely impressed. Tergum 7 with anterior border modified for openings to abdominal gland ducts. Tergum 10 with setal patch more or less square; setae few to moderate in number, not flattened or subspatulate.

**Aedeagus.** (Figures 199, 200). Median lobe with apical process simple, not markedly modified. Flagellum slender, tubular. Parameres not markedly modified (Figures 220, 221).

**Spermatheca.** Typical of subtribe, simple (Figure 182).

**Secondary sexual characters.** Males of known species with posterior margin of tergum 8 with four slender spiniform processes.

**Discussion.**— Similarities in ligula structure, meso-metasternal processes, maxillary structure, general body form and aedeagal structure indicate that the Holarctic members of *Encephalus* form a monophyletic group. However, *Encephalus zealandicus* Cameron and *E. laetulus* Broun, while superficially similar in habitus to Holarctic species, differ from the description given above in a number of ways, including: smaller size (adults 1.1 to 1.3 mm in length); antennae longer, with club formed from antennomeres 5-10 less incrassate; lateral margins of pronotum not as markedly deflexed; pronotum hind margin not emarginate medially; elytra very markedly sinuate on lateral apical angles; terga and paraterga not as markedly widened, abdomen not as robust; terga, paraterga and lateral margins of sterna with long, dark macrosetae; mesosternal process extended only 4/5 distance to posterior margin of middle coxae; labium with ligula very elongate, protruded, parallel-sided and entire (Figure 104); and different form of median lobe of aedeagus (Figure 201). Either the concept of *Encephalus* will have to be modified, or, as seems more likely, the New Zealand forms will have to be placed in a separate genus. Decision about which of these should be done requires a great deal more material than is available to me, and more comprehensive comparative studies within *Gyrophaena*, to which these forms are probably related. These studies are outside the scope of this treatment, and I only call attention to the problem here.

Relationships of *Encephalus* are unclear. The broad, undivided ligula is similar to that found in members of the "*Brachida*" lineage. However, in maxillary structure and many body

characteristics, specimens of *Encephalus* are more similar to many members of *Gyrophaena*. The median lobe of the aedeagus of *E. americanus* Seevers and *E. complicans* Kirby is remarkably similar to that found in members of the *G. nana* species group of Seevers (1951).

*Natural history*.— Members of *Encephalus* are seldom found on fresh mushrooms. They are usually encountered in hay, rotting grass and hillocks in bogs (Lohse, 1974).

*Immature stages*.— These have not been described.

*Distribution*.— Four species are known from the Palearctic region, one described species from the Nearctic region, and two described species from New Zealand (but see discussion above).

*Major literature*.— There is no comprehensive revision of the species of *Encephalus*. *E. americanus* Seevers is well described and illustrated by Seevers (1951) and *E. complicans* Kirby is well described and illustrated in a number of places in the European literature (e.g. Lohse, 1974).

### *Probrachida* new genus

Figs. 27, 37–41, 62–64, 81–84, 105–107, 168, 184, 202, 203, 222, 223, 224

*Probrachida* new genus. Type species: *Probrachida modesta* (Sharp) (from *Brachida*). Fixed here by original designation.

*Diagnostic combination*.— Relatively large (adults 2.5 to 3.5 mm in length), more or less robust to parallel-sided. Head deflexed, oblique. Pronotum with apico-lateral margins deflexed, convex in cross section; hypomera not visible in lateral view; hind margin emarginate medially. Labium with ligula entire, broadly rounded; medial setae 2. Maxilla with setae on inner face of lacinia numerous, scattered, in most specimens; inner face of lacinia with additional teeth or spines (Figures 81–84). Galea with setae on apex in many very close rows; setae unmodified, filiform (Figures 83, 84). Aedeagal form distinctive (Figures 202, 203).

*Description*.— Length of adults 2.5 to 3.5 mm. Body robust, elongate, oval in dorsal aspect, or more or less parallel-sided. Sculpture reticulate to obsoletely reticulate, surface subshining to shining. Microsetae moderately short, densely arranged, body pubescent, or microsetae long, silky and very densely arranged, body subhirsute; punctures small, inconspicuous to large, distinct. Macrosetae small, inconspicuous to obsolete.

*Head*. Slightly transverse, slightly or moderately deflexed to oblique plane; reticulate to obsoletely reticulate throughout; microsetae moderate in size to long and silky, densely arranged; macrosetae absent. Eyes moderate in size. Infraorbital carina complete, moderately to markedly developed. Neck carina well developed. Antenna as long as head, prothorax and 1/2 of elytra together; antennomere 4 elongate, similar to 5–10 or similar to 1–3 (Figure 27), or intermediate in some; 5–10 elongate or 7–10 subquadrate; antenna parallel-sided from antennomeres 3–10 or 4–10.

*Mouthparts*. Labrum (Figures 37–41) with major setae distinct and moderately well developed, or difficult to distinguish from numerous accessory setae; lateral sensilla row well developed, of five to seven small, spine-like sensilla, at lateral margin; medial sensory area with sensilla variously developed. Mandibles (Figures 62–64) both, left only, or neither bifid at apex, right with or without an internal tooth; prosthema typical of subtribe or with medio-internal area of fimbriate fringes of spine-like rather than bifid structures. Maxilla (Figures 81–84) with apex of lacinia truncate with well developed “spore brush”, spines more or less numerous and long; setae on inner face of lacinia numerous to few, scattered or in single irregular row; inner face of lacinia with few spines on margin proximal to spore brush; galea with apical setae in numerous close rows, setae filiform. Labium (Figures 105–107) with ligula broadly rounded, entire; medial setae two.

*Thorax*. Pronotum moderately transverse, 1.6 to 1.9 times as wide as long; convex, antero-lateral margins markedly deflexed in some; apical angles and anterior margin broadly rounded; posterior angles obtuse; posterior margin very slightly or not at all bisinuate, emarginate medially; sculpture reticulate or obsoletely reticulate; microsetae moderate in size or long and silky, densely arranged; macrosetae small to obsolete. Elytra with apico-lateral angles not sinuate, setae long, silky, densely arranged; punctures small or large, uniformly distributed. Prosternum slightly transverse, with very slight transverse carina or carina absent; without medial knob, carina or protuberance. Mesosternum broad in front of coxae; with marked medial longitudinal carina or carina absent or with low diffuse ridge medially. Mesosternal process very wide, extended to posterior margin of middle coxal cavities, apex truncate. Metasternal process not or very slightly extended between coxal cavities. Suture between meso- and metasternal processes complete, not fused, slightly beaded in some, or more or less fused. Metepisternum with setae numerous, in two or more irregular rows or single row anteriorly and two irregular rows posteriorly; setal punctures large, conspicuous, or moderate in size; setose area in deep groove or not, with slight antero-ventral carina or not. Tarsomere 1 of hind tarsus 1.3 to 2.0 times as long as tarsomere 2; with or

without ventro-lateral ctenidium.

*Abdomen.* Broadly oval, elongate oval or more or less parallel-sided in dorsal aspect; more or less densely pubescent. Terga 3-5 slightly transversely impressed. Sterna not modified. Tergum 7 modified for openings to abdominal gland ducts. Tergum 10 (Figure 168) with setal patch more or less square; setae numerous, not flattened.

*Aedeagus.* (Figures 202, 203). Median lobe with apical process small, laterally flattened, blade-like or reduced; flagellum long, exerted, whip-like. Parameres not extensively modified, or apical process with accessory setae.

*Spermatheca* (Figure 184). Neck elongate proximal to plate-like flange, or neck elongate and coiled and flange obsolete.

*Secondary sexual characters.* Posterior margin of tergum 8 of male broadly, shallowly emarginate. Female unmodified, or broadly, shallowly emarginate.

*Discussion.*— Except for similarities in the broad, entire ligula and general habitus, New World species of *Brachida* described by Sharp (1883) share few characteristics with Old World *Brachida* as typified by *B. notha* (Erichson) and *B. exigua* Heer. Two medial setae on the labium, accessory teeth on the inner face of the lacinia, more rows of setae on the galea, and very different form of secondary sexual characteristics and median lobe of the aedeagus, seem to warrant placing the New World *Brachida* in a separate genus. The taxon *Probrachida* new genus is here proposed to contain these New World species. It is possible that *Probrachida* might prove to be a subgenus of *Brachida* Mulsant and Rey with additional study. However, available data do not support this conclusion. In particular, the different number of medial setae on the labium and very different forms of the median lobe of the aedeagus of members of these two taxa suggest that they are not very closely related.

Relationships of *Probrachida* are not well understood. In mouthpart structure, members of *Probrachida* are more plesiotypic than any other gyrophaenine. *Probrachida* may be the sister group to all other Gyrophaenina (Figure 252) or the sister group to *Brachida* (Figure 253). If the latter, then *Probrachida* and *Brachida* together would form the sister group to all other Gyrophaenina.

*Type species.*— *Brachida modesta* Sharp 1883:265 is here designated as the type species of *Probrachida* new genus. *B. modesta* is chosen for two reasons: it appears first in the text (Sharp 1883) and there are more specimens in the syntype series of this species (15 specimens, including both males and females) than for any other member of the genus. The syntype series is in the collection of the British Museum (Natural History).

*Included species.*— The following species are transferred from *Brachida* Mulsant and Rey to *Probrachida* new genus:

*Probrachida batesi* (Sharp 1876:49) new comb.

*Probrachida carinata* (Sharp 1883:266) new comb.

*Probrachida geniculata* (Sharp 1883:266) new comb.

*Probrachida modesta* (Sharp 1883:265) new comb.

*Probrachida reyi* (Sharp 1876:49) new comb.

*Probrachida sparsa* (Sharp 1883:266) new comb.

*Brachida importuna* Erichson (1839-40) from Colombia, *B. sexualis* Bernhauer (1922) from Bolivia, and *B. timidula* Erichson (1839-40) from Colombia may also belong to *Probrachida*, but I have not had opportunity to examine specimens of these species,

*Natural history.*— Nothing is known of the natural history of members of *Probrachida*.

*Immature stages.*— Undescribed.

*Distribution.*— Species of *Probrachida* are known only from the New World tropics or subtropics. Four species are known from Central America, and two from the Amazon region.

*Major literature.*— Species here included in *Probrachida* have not been discussed except in the original descriptions by Sharp (1876, 1883). Sharp's descriptions are superficial and he provides no keys to species or figures of structural features.

*Brachida* Mulsant and Rey

Figs. 15, 42-46, 65, 85-87, 108, 109, 158, 185, 204-206, 225

*Brachida* Mulsant and Rey 1872:94. Type species: *Brachida notha* (Erichson) (from *Homalota*). Fixed by Mulsant and Rey 1872:94 by monotypy. —Mulsant and Rey 1872:94. —Fauvel 1875:646. —Ganglbauer 1895:305. —Casey 1906:279. —Reitter 1909:86. —Fenyés 1918-21:92. —Cameron 1939:50. —Lohse 1974:26.

**Diagnostic combination.**— More or less robust, elongate-oval in dorsal aspect. Body macrosetae long, more or less silky, body markedly pubescent. Head deflexed into more or less oblique plane; base covered by anterior margin of prothorax. Pair of macrosetae present on vertex of head. Maxilla with setae on inner face of lacinia numerous, in single row or scattered; inner face of lacinia without teeth; setae on apex of galea in numerous to few close rows, setae unmodified, filiform. Labium with ligula broadly rounded, entire. Spermatheca (Figure 185) and aedeagus (Figures 204-206) form distinctive.

**Description.**— Length of adult 1.5 to 2.7 mm. Body robust, elongate-oval in dorsal aspect. Surface sculpture reticulate or smooth; integuments shining to subshining. Microsetae long, silky, densely arranged and body very pubescent, or microsetae shorter and body slightly pubescent; punctures small to moderate.

**Head** (Figure 15). Slightly transverse, oval, deflexed into more or less oblique plane; microsetae numerous, closely arranged, long or short; macrosetae pair on vertex or not, setae large, conspicuous, or small, inconspicuous. Infraorbital carina complete, well developed. Neck carina slightly developed. Antenna various, as long as head and pronotum together, to as long as head, pronotum and 1/2 elytra together; antennomere 4 elongate, quadrate or slightly transverse; 5-10 elongate or more distal antennomeres subquadrate to quadrate.

**Mouthparts.** Labrum (Figures 42-46) with major setae well developed or difficult to distinguish from numerous accessory setae, lateral sensilla rows of three to five spiniform sensilla, near to slightly distant from lateral margin; medial sensory area with sensilla well developed. Mandibles (Figure 65) with left bifid at apex or not, right not bifid; right with well developed internal tooth. Prostheca typical of subtribe or medial internal fringe with processes spiniform rather than bifid. Maxilla (Figures 85-87) with apex of lacinia obliquely truncate, with well developed "spore brush"; setae on inner face of lacinia numerous to few, in single row or scattered; inner face of lacinia without teeth, with two or three hyaline sensilla; galeal setae in few to numerous close rows, setae filiform, not flattened. Labium (Figures 108, 109) with ligula entire, produced as broadly rounded lobe; single medial seta.

**Thorax.** Prothorax moderately transverse, 1.6 to 1.9 times as wide as long, convex, anterior angles and sides depressed; hypomera not visible in lateral aspect; more or less broadly oval in dorsal aspect; posterior margin not bisinuate to very slightly sinuate, emarginate medially or not; sculpture reticulate, obsolete reticulate or smooth; microsetae numerous, long to more or less short, densely arranged; macrosetae large, conspicuous, to small, inconspicuous, or obsolete. Elytral apico-lateral angles not to slightly sinuate. Prosternum slightly to moderately transverse, with or without slight transverse ridge; without medial knob, carina or protuberance. Mesosternum broad in front of coxae, without medial longitudinal ridge along midline. Mesosternal process long, extended to apex of middle coxal cavities, apex truncate or slightly emarginate. Metasternal process extended slightly between middle coxal cavities or not. Suture between meso- and metasternal processes complete, not fused. Metepisternum (Figure 158) with setae numerous, scattered, or in two irregular rows; setose area not margined antero-ventrally by carina or with faint carina. Tarsomere 1 of hind tarsus 1.3 to 2.0 times as long as tarsomere 2; with ventro-lateral ctenidium.

**Abdomen.** Elongate oval in dorsal aspect, robust; more or less densely pubescent or with few scattered setae. Terga 3-5 or 3-6 moderately to slightly transversely impressed. Sterna not modified. Anterior margin of tergum 7 modified for openings to abdominal gland ducts. Tergum 10 with setal patch more or less square; setae numerous, not flattened.

**Aedeagus** (Figures 204-206, 225). Distinctive; median lobe with apical process small; flagellum long, slender, coiled internally within median lobe.

**Spermatheca** (Figure 185). Distinctive; typical of subtribe, neck elongate, coiled distal to lateral flange.

**Secondary sexual characteristics.** Males with posterior margin of tergum 8 broadly sinuate or emarginate. lateral margins of sinuation produced as spines or not; sinuation with or without medial spinose processes; tergum 7 with or without slight medial knob. Females unmodified.

**Discussion.**— *Brachida* Mulsant and Rey requires comprehensive study on a world-wide basis. Many species have been described from all parts of the world except America north of Mexico. I think that all New World species should be in the genus *Probrachida* (see discussion under that genus). It is uncertain which of the remaining described species should be included in *Brachida*. It appears from the very distinctive autapotypic structure of the spermatheca and median lobe of the aedeagus, that the group characterized by these features is monophyletic. I have examined specimens of a number of species of *Brachida* from widely separate localities

and found the distinctive features of these characters to be uniform. Therefore, I think that many of the described species should be included in the same genus as the European forms of *Brachida*. However, it also appears that many species have been incorrectly assigned to *Brachida*. For example, *Brachida elevata* Fauvel is a *Sternotropa* and *Brachida zealandica* Bernhauer is not a gyrophaenine (10-articled antenna indicates that it should probably be placed in the tribe Oligotini).

Relationships of *Brachida* are uncertain. It may be hypothesized to be either the sister group to *Probrachida*, or the sister group to the "*Sternotropa*" + "*Gyrophaena*" lineages. Members of *Brachida* are highly autapotypic in many structural features (including spermathecal and aedeagal structure) and relatively plesiotypic in mouthpart structure (particularly structure and arrangement of setae on the galea and lacinia of the maxilla; see Phylogenetic Analysis for a detailed discussion).

*Natural history*.— Little is known of the natural history of species of *Brachida*. They are occasionally found on fungi (usually associated with wood) (Benick, 1952), but Lohse (1974) gives the habitat of *Brachida exigua* Heer as grass tufts and ground litter, and Cameron (1939) states that specimens of *Brachida* are found in moss and dead leaves in addition to fungi.

*Immature stages*.— Undescribed.

*Distribution*.— If New World forms of *Brachida* are moved to *Probrachida*, then the numerous remaining species are found throughout the Old World. Species are known from Europe, Africa, India, Southeast Asia, Japan, New Caledonia, Australia and New Zealand.

*Major literature*.— There is no comprehensive discussion with complete keys and descriptions of species of *Brachida* of any region except India (Cameron 1939) and Europe (Lohse, 1974, and others).

### *Agaricochara* Kraatz

Figs. 16, 47, 66, 88, 110, 126, 146, 152, 169, 186, 207, 226

*Agaricochara* Kraatz 1856:361. Type species: *Agaricochara laevicollis* Kraatz. Fixed by Kraatz 1856:361 by monotypy.

—Kraatz 1856:361. —Mulsant and Rey 1871:90. —Ganglbauer 1895:304. —Casey 1906:278. —Reitter 1909:85. —Fenyés 1918-21:92. —Scheerpeltz 1930:70. —Seever 1951:740. —Lohse 1974:130. —White 1977:304. —Seever 1978:163.

*Diagnostic combination*.— Small beetles, adults 1.2 to 1.5 mm in length; surfaces reticulate, with short pubescence throughout. Head almost round in dorsal aspect, 1.1 times as wide as long. Pronotum moderately transverse, 1.6 to 1.7 times as wide as long. Mesosternum with medial longitudinal carina to 1/2 distance to apex of mesosternal process. Mesosternal process extended 2/3 distance to base of middle coxae, separated from metasternal process by very short isthmus; Ms.P:I:Mt.P=7:0.5:4. Maxilla with setae on inner face of lacinia numerous, scattered; setae on apex of galea in four distinct rows, setae flattened. Labium with ligula protruded, parallel-sided, bifid 1/3 to 1/2 distance to base; single medial seta. Aedeagus form distinctive (Figure 207).

*Description*.— Small beetles, adults 1.2 to 1.5 mm in length; more or less flattened and parallel-sided. Sculpture reticulate throughout; integument subshining to dull. Macrosetae short, more or less densely arranged throughout; punctures small to moderate.

*Head*. (Figure 16). Round to slightly transverse in dorsal aspect, 1.0 to 1.1 times as wide as long; not or slightly deflexed to oblique plane; tempora large, broadly rounded to base of head; microsetae numerous, short, more or less densely arranged; macrosetae absent. Eyes moderate in size. Infraorbital carina present, slightly developed. Neck carina present, slightly developed. Antenna longer than head and prothorax together; antennomeres 4 similar to 1-3, elongate; 5-7 longer than wide; 8-10 subquadrate to quadrate.

*Mouthparts*. Labrum (Figure 47) with major setae distinct; without accessory setae; lateral sensilla row with two to four slightly developed spiniform sensilla, distant from lateral margin; medial sensory area with sensilla well developed.

Mandibles (Figure 66) not bifid at apex; right with slight internal tooth. Prostheca typical of subtribe. Maxilla (Figure 88) with apex of lacinia obliquely truncate, with well developed spiniform "spore brush", teeth small, close, densely arranged; setae on inner face of lacinia more or less numerous, scattered; setae on apex of galea in four distinct rows, setae flattened. Labium (Figure 110) with ligula protruded, parallel-sided, bifid 1/3 to 1/2 distance to base, single medial seta.

*Thorax.* Prothorax (Figure 126) moderately transverse, 1.6 to 1.8 times as wide as long, slightly convex; antero-lateral angles slightly depressed; hypomera very narrowly visible in lateral aspect or not; posterior margin slightly bisinuate, not emarginate medially; sculpture reticulate; microsetae numerous, small, uniformly and densely distributed; macrosetae small, inconspicuous. Elytral apico-lateral angles not or slightly sinuate. Prosternum (Figure 146) moderately transverse, with fine transverse carina; without medial knob, carina or protuberance. Mesosternum with moderate medial longitudinal carina to 1/2 distance to apex of mesosternal process. Mesosternal process extended 2/3 distance to base of middle coxae, separated from metasternal process by a very short isthmus; Ms.P:I:Mt.P ratio = 7:0.5:4. Metepisternum with setae in single row, margined antero-ventrally by slight carina. Tarsomere 1 of hind tarsus 1.2 to 1.3 times as long as 2, with slight ventro-lateral ctenidium of six or seven setae.

*Abdomen.* Parallel-sided or sides slightly convergent from base to apex. Terga 3-5 moderately to slightly transversely impressed. Sterna not modified. Anterior margin of tergum 7 modified for opening to abdominal gland ducts. Tergum 10 (Figure 169) with setal patch more or less square; setae short, setiform or slightly flattened.

*Aedeagus.* (Figure 207). Distinctive. Median lobe with apical process large, elongate; flagellum hook-like, more or less sclerotized. Apical sclerite of paramere elongate (Figure 226).

*Spermatheca* (Figure 186). Typical of subtribe, simple.

*Secondary sexual characteristics.* Males with tergum 8 broadly sinuate; lateral margins of sinuations produced as spine-like processes; sinuation with small denticle on each side of midline.

*Discussion.*— The concept of the genus *Agaricochara* is considered here in a very restricted sense in comparison to that of Seevers (1951) and White (1977). Inclusion of a number of New World species within *Agaricochara* Kraatz as done by Seevers (1951), and inclusion of the subgenus *Phaenogyra* Mulsant and Rey of *Gyrophana* as done by White (1977) makes *Agaricochara* a polyphyletic assemblage. In the restricted sense considered here, *Agaricochara* is made up of only two European species, *A. laeivcollis* Kraatz and *A. aspera* Fauvel. Similarities in the aedeagus of these two species, in addition to other shared character states, provide strong evidence that these two form a monophyletic group. Members of the subgenus *Phaenogyra* are certainly members of *Gyrophana* rather than *Agaricochara*, as indicated by the protruded, undivided ligula of members of *Phaenogyra*. Seevers (1951) described several species of North American gyrophanines as *Agaricochara*. He based his concept of *Agaricochara* principally on antennal structure and presence of a markedly transverse pronotum. However, among those species placed in *Agaricochara*, Seevers included some which have members with an entire ligula (e.g., *G. hubbardi* Seevers) and some which have members with a divided ligula (e.g., *G. apacheana* Seevers). The North American species with divided ligulae appear to be more closely related to *Sternotropa* Cameron and *Brachychara* Sharp than to *Agaricochara* Kraatz, and they differ substantially in aedeagal structure from the latter. I have, therefore, removed these North American species from *Agaricochara* (see discussion under *Agaricomorpha* new genus).

Relationships of *Agaricochara* are uncertain. The most parsimonious arrangement at present is inclusion of this genus in the "*Sternotropa*" lineage based on the hypothesis that the divided ligula of these taxa is an autapotypy. However, this placement requires considerable parallel development of apotypic conditions with members of the "*Gyrophana*" lineage. (See discussion in the Phylogenetic Analysis for a more detailed consideration of this problem.)

*Natural history.*— Members of *Agaricochara* are most commonly found in association with fleshy or leathery polypore mushrooms on logs (Donisthorpe, 1935; Scheerpeltz and Höfler, 1948; Benick, 1952).

*Immature stages.*— White (1977) described the larva of *A. laeivcollis* Kraatz.

*Distribution.*— The two species in this genus are known from Europe.

*Major literature.*— No comprehensive discussion of members of *Agaricochara* is available, but *A. laeivcollis* is well described and illustrations of structural features are available in Lohse



(1974), Seevers (1951), Scheerpeltz and Höfler (1948) and included references.

*Sternotropa* Cameron

Figs. 17, 48-50, 67-69, 89-91, 111, 112, 127, 135, 147, 153, 170, 171, 187, 208, 209, 227, 228

*Sternotropa* Cameron 1920b:220. Type species: *Sternotropa nigra* Cameron 1920b:220. Fixed by Blackwelder 1952:360 by subsequent designation. —Cameron 1920b:220. —Cameron 1939:142.

**Diagnostic combination.**— Small beetles (adults 1.1 to 1.7 mm in length); body form slightly limuloid, sides of abdomen convergent to more or less pointed apex; body moderately to slightly pubescent, microsetae more or less uniformly distributed. Pronotum markedly transverse, 1.8 to 2.1 times as wide as long. Pronotum posterior margins markedly bisinuate. Mesosternum with medial longitudinal carina, complete or obsolete in apical 1/3. Mesosternal process extended to middle or slightly posterior to middle of mid-coxae; suture between meso- and metasternal processes complete or more or less fused. Maxilla with setae on inner face of lacinia numerous or few, in single row or scattered; setae on apex of galea in four clearly separated rows, setae flattened. Labium with ligula bifid, divided almost to base. Aedeagal form distinctive (Figures 208, 209).

**Description.**— Length 1.1 to 1.7 mm. Body broadest near middle of elytra, abdomen tapered to more or less pointed apex; flattened to slightly robust; sculpture reticulate to smooth, integument shining to subshining; sparsely to moderately to more or less densely pubescent; microsetae short to moderate, fine, more or less uniformly distributed; punctures fine to very fine, asperate or not; macrosetae small, inconspicuous, obsolete, or large and conspicuous.

**Head** (Figure 17). Transverse to markedly transverse; held more or less in plane of body to slightly inclined; sculpture reticulate to smooth; microsetae short, moderately numerous to sparse, uniformly distributed; punctures fine to minute; macrosetae absent. Eyes moderate in size. Infraorbital carina present, markedly to moderately developed, complete or obsolete antero-ventrally. Neck carina present, more or less slight, obsolete ventrally. Antenna with antennomere 4 similar in setation and general shape to 1-3, and subquadrate to transverse; 5 slightly elongate, quadrate or transverse; 6-10 more or less transverse.

**Mouthparts.** Labrum (Figures 48-50) with major setae well developed, without accessory setae; lateral sensilla row with one to three slightly developed spine-like sensilla, or sensilla row absent; sensilla of medial sensory area well developed. Mandibles (Figures 67-69) typical of subtribe; not bifid at apex; right mandible with small internal tooth or tooth obsolete. Maxilla (Figures 89-91) with apex of lacinia obliquely truncate, more or less broad, with well developed "spore brush"; teeth of spore brush small, very numerous and densely arranged; inner face of lacinia with single irregular row of moderately sized setae, or setae more or less scattered; two or three large hyaline setiform sensilla present or absent, galea with apical setae in four distinct rows, setae subspatulate to plate-like. Labium (Figures 111, 112) with ligula bifid, divided almost to base; and broadly pointed apically or sides converged to sharp point apically; single medial seta.

**Thorax.** Prothorax (Figure 127) markedly transverse, approximately 2.0 times as wide as long; slightly to moderately convex in cross-section, sides moderately depressed, anterior angles depressed; hypomera not visible in lateral view; anterior border straight or broadly rounded; latero-apical angles obtusely angulate or broadly rounded; sides broadly convergent from near baso-lateral angles to apico-lateral angles; posterior border moderately to markedly bisinuate, not emarginate medially; sculpture reticulate to smooth, integument subshining to shining; microsetae moderate to numerous, sparse to densely, uniformly distributed; punctures small to fine, asperate or not; macrosetae very small, inconspicuous or obsolete on disc, or one or more lateral setae more or less large and conspicuous. Elytra (Figure 135) with sutural length equal to or slightly less than pronotal length. Outer apical angles moderately to markedly sinuate; integument reticulate to smooth, subshining to shining; microsetae small, moderate to numerous, sparse to moderately densely, uniformly distributed; macrosetae very small, obsolete or lateral two or three setae large, conspicuous. Prosternum (Figure 147) transverse, without faint transverse carina; with medial knob, protuberance or spine. Mesosternum with medial longitudinal carina, complete to apex of mesosternal process or more or less obsolete in apical 1/3. Mesosternal process moderately broad, extended between middle coxal cavities to middle or slightly posterior to middle of coxal cavities. Metasternal process extended anteriorly to broad contact with mesosternal process; suture complete, or, in specimens of most species, more or less fused and indistinct (Figure 153); isthmus absent. Metepisternum with setae few to moderately numerous, scattered in one or two irregular rows; setose area not delimited by fine carina. Hind tarsus with tarsomere 1 1.0 to 1.5 times as long as 2.

**Abdomen.** Flattened to slightly robust, sides more or less convergent from broad base to narrow apex; terga not transversely impressed (slightly developed carina present or not on 3-5), or 3-6 more or less slightly impressed. Tergum 10 (Figures 170, 171) with medial setose patch chevron-shaped; setae in two distinct oblique rows (third indistinct row present in some); rows convergent to point proximally or setae more numerous and in three or four well developed rows.

*Aedeagus* (Figures 208, 209). Similar to that found among species of *Pseudoligota*. Apical lobe markedly modified and complex or not; flagellum long, slender, whip-like; emergent near base of median lobe, curved proximally and extended apically in groove in functionally ventral surface. Parameres (Figures 227, 228) with two setae of apical sclerite enlarged, near base of sclerite.

*Spermatheca* (Figure 187). Typical of subtribe; unmodified, simple.

*Secondary sexual characteristics*. Various. Males with posterior margin of tergum 8 broadly to narrowly emarginate, lateral margins of emargination more or less prolonged as blunt teeth or not, emargination medially with or without one or more small teeth or lobes; tergum 7 with pair of small spines medially or not. Female unmodified or with posterior margin of tergum 8 with two short, blunt teeth separated by broad semicircular emargination.

*Discussion*.— *Sternotropa* Cameron is most closely related to *Pseudoligota* Cameron, as indicated by similarities in the median lobe of the aedeagus (see discussion in Phylogenetic Analysis) and has close, but uncertain, affinities with *Adelarthra* Cameron.

*Natural history*.— No information about natural history of *Sternotropa* is available. Based on structure of the spore brush of the maxilla, and habitat preferences of related gyrophaenines (see Table 4), it is likely that members of *Sternotropa* are most common on fleshy or leathery polypore mushrooms.

*Immature stages*.— Undescribed.

*Distribution*.— Members of *Sternotropa* are known from India, Southeast Asia, Fiji, Sumatra and Malaya.

*Major literature*.— Cameron (1939) gives keys and descriptions for the Indian species.

### *Pseudoligota* Cameron

Figs. 18, 51, 52, 70, 92, 113, 128, 136, 154, 159, 172, 173, 188, 210, 211, 229

*Pseudoligota* Cameron 1920b:213. Type species: *Pseudoligota varians* Cameron 1920b:213. Fixed by Blackwelder 1952:327 by subsequent designation. —Cameron 1939:145.

*Diagnostic combination*.— Minute to very small (adults 0.8 to 1.2 mm in length). Body slightly limuloid, widest at base of thorax, sides of abdomen convergent from base to apex. Body moderately to slightly pubescent, microsetae short, uniformly distributed. Pronotum moderately to markedly transverse, 1.8 to 2.0 times as wide as long; slightly to moderately convex in cross section; hypomera not visible in lateral aspect; posterior margin moderately to slightly bisinuate. Elytral apico-lateral angles slightly to moderately sinuate. Mesosternum without medial longitudinal carina. Meso- and metasternal processes fused and indistinguishable. Maxilla with inner face of lacinia with single row of setae; setae on apex of galea in four widely separated rows, setae flattened, subspatulate. Labium with ligula bifid, divided 2/3 to 3/4 distance to base; single medial seta. Aedeagal form distinctive (Figures 210, 211).

*Description*.— Minute to very small beetles, length of adults 0.8 to 1.2 mm. Body slightly limuloid; widest at base of thorax, broadly rounded to head anteriorly, sides of abdomen convergent from base to apex or not; slightly robust to not robust. Body sculpture reticulate to smooth; integument dull to shining. Body moderately to more or less markedly pubescent, microsetae short, more or less closely spaced and uniformly distributed, punctures small to minute, asperite or not; macrosetae very small, inconspicuous, apparently absent from specimens of some species.

*Head* (Figure 18). Transverse, more or less broadly oval in cross-section, more or less inclined ventrally from plane of body. Sculpture reticulate to smooth. Microsetae short, numerous, uniformly distributed; punctures fine to minute; macrosetae absent. Eyes moderate in size. Infraorbital carina slightly developed, complete ventrally or obsolete antero-ventrally. Neck carina slight, obsolete ventrally. Antenna with antennomere 4 similar to 1-3; antennomeres 4-10 transverse, each more so than the preceding.

*Mouthparts*. Labrum (Figures 51, 52) without accessory setae; lateral sensilla row absent; sensilla of medial sensory area well developed. Mandibles (Figure 70) typical of subtribe; not bifid at apex, right with small tooth internally or tooth obsolete. Maxilla (Figure 92) with apex of lacinia obliquely truncate with well developed "spore brush"; teeth of spore brush small, numerous, densely arranged; inner face of lacinia with single row of moderately sized setae and two or three large, hyaline setiform sensilla; galea with apical setae in four well separated rows, setae subspatulate to plate-like. Labium (Figure 113) with ligula bifid, divided 2/3 to 3/4 distance to base; lobes of ligula short, sides convergent to point

apically. Medial seta single or absent.

**Thorax** (Figure 128). Pronotum markedly transverse, 1.8 to 2.0 times as wide as long; slightly to moderately convex in cross-section; sides moderately depressed; hypomera not visible in lateral aspect; anterior border straight, apical angles more or less obtusely angulate; posterior border moderately to slightly bisinuate, not emarginate medially; sculpture reticulate or smooth, integument dull to shining; microsetae short, numerous, more or less densely and uniformly distributed; punctures fine to minute, asperate or not; macrosetae very small, inconspicuous, or absent. Elytra (Figure 136) equal to or shorter than pronotal length; apico-lateral angles moderately to slightly sinuate; integument reticulate to smooth, dull to shining; microsetae small, numerous, densely and uniformly distributed; punctures very fine, asperate or not; macrosetae very small, inconspicuous or absent. Prosternum transverse to markedly transverse; without transverse carina; with or without low medial knob or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process moderately broad, extended between middle coxal cavities and fused to metasternal process, processes indistinguishable (Figure 154). Middle coxal cavities moderately separated. Metepisternum with setae moderately numerous, in two irregular rows; setose area not delimited by fine carina. Hind tarsus with tarsomere 1 about as long as 2; ventro-lateral edge with ctenidium of four to six setae.

**Abdomen** Flattened to slightly robust, sides slightly to moderately convergent from base to apex. Terga not transversely impressed with indistinct transverse carinae on 3-5. Tergum 10 (Figures 172, 173) with medial setose patch square (Figure 173) or with posterior edge broadly incised (Figure 172); setae short, stubby, not flattened.

**Aedeagus** (Figures 210, 211). Distinctive. Median lobe with flagellum emergent near base of bulb, curved proximally around base of median lobe, and extended apically in groove in functionally ventral surface. Parameres (Figure 229) with two proximal setae of apical sclerite enlarged, near base of sclerite.

**Spermatheca** (Figure 188). Typical of subtribe; unmodified, simple.

**Secondary sexual characteristics.** Males with posterior margin of tergum 8 with broad blunt tooth; tergum 7 with faint median longitudinal carina or not; elytra markedly asperate distally near suture and/or near lateral margin or not. Female unmodified or with posterior margin of tergum 8 with broad lobe.

**Discussion.**— Many members of *Pseudoligota* are among the smallest aleocharines and thus among the smallest beetles.

*Pseudoligota* is most closely related to *Sternotropa* and *Adelarthra* (see discussion under *Sternotropa* and in Phylogenetic Analysis).

**Natural history.**— Cameron (1939) reports that members of some species of *Pseudoligota* have been found on "Polyporus". A few specimens have been collected on rotting fruit, in rotting fungus, and under bark (label data).

**Immature stages.**— Undescribed.

**Distribution.**— Known from India and Southeast Asia.

**Major literature.**— Cameron (1939) provides a key to and descriptions of the Indian species.

### *Neobrachida* Cameron

Fig. 115

*Neobrachida* Cameron 1920a:51. Type species: *Neobrachida castanea* Cameron 1920a:51. Fixed by Cameron 1920a:51 by monotypy. —Cameron 1939:55.

**Diagnostic combination.**— Length of adult 2.3 mm. Body more or less parallel-sided; sculpture smooth, integuments markedly shining; body sparsely pubescent, microsetae small, number and distribution different on different areas of body. Pronotum moderately transverse, 1.7 times as wide as long, slightly convex in cross-section; sides moderately convex, hypomera not visible in lateral aspect; pronotal posterior margin slightly bisinuate. Elytral apico-lateral angles moderately bisinuate. Mesosternum with diffuse, low, medial longitudinal carina. Mesosternal process extended to posterior 1/3 of mid-coxal cavities. Metasternal process extended between coxae, truncate at contact with mesosternal process; suture between meso- and metasternal processes complete, unmodified. Labium with ligula elongate, as long as first palpomere, parallel-sided, bifid in apical 1/3; lobes of ligula narrow, pointed, divergent; single medial seta.

*Description.*— Length of adult 2.3 mm. Body more or less parallel-sided, sides slightly convergent posteriorly; more or less flattened, not robust; sculpture smooth, integument markedly shining; sparsely pubescent; microsetae small, fine, number various on different body regions; punctures very fine; macrosetae various on different body regions, small, inconspicuous, or large and conspicuous.

*Head.* Transverse; microsetae small, very sparse; punctures very fine; macrosetae absent. Infraorbital carina moderately developed, complete ventrally. Neck carina well developed. Antenna with antennomere 4 similar in setation and general shape to 1-3; antennomere 4 transverse; 5-10 transverse, each slightly wider than preceding, antenna slightly incrassate from antennomere 4 to apex.

*Mouthparts.* Labrum not observed. Mandibles not observed. Maxilla with apex of lacinia truncate, with well developed "spore brush"; teeth numerous and closely spaced; galea not observed. Labium (Figure 115) with ligula slender, elongate, almost as long as palpomere 1, parallel-sided, bifid in apical 1/3, lobes narrow, pointed, divergent; single medial seta.

*Thorax.* Prothorax moderately transverse, 1.7 times wider than long; slightly convex in cross-section, sides moderately depressed; hypomera not visible in lateral view; anterior border broadly rounded; latero-apical angle broadly rounded; posterior border slightly bisinuate; microsetae small, sparse, uniformly distributed; punctures very fine; macrosetae small, inconspicuous except L3 large and conspicuous. Elytra at suture longer than pronotal length; apico-lateral angles moderately sinuate; microsetae sparse, uniformly distributed, punctures fine; three lateral macrosetae large, conspicuous. Prosternum moderately transverse, without transverse carina; with medial protuberance. Mesosternum without medial longitudinal carina, but low diffuse ridge along midline; ridge extended to apex of mesosternal process. Mesosternal process extended to posterior 1/3 of mid-coxal cavities. Metasternal process truncate at contact with mesosternal process; suture complete, unmodified; isthmus absent. Metepisternum with setae numerous, scattered in two irregular rows; setose area not delimited below by carina. Hind tarsus with first tarsomere 1.4 times as long as second.

*Abdomen.* Sides subparallel, very slightly convergent from base to obtusely rounded apex. Terga 3-5 (6 faintly) with moderate to slight transverse impressions. Tergum 10 with medial setose patch chevron-shaped; setae in two distinct oblique rows convergent to point proximally (similar to Figure 170).

*Aedeagus.* Unknown.

*Spermatheca.* Unknown.

*Secondary sexual characteristics.* Male unknown. Female with posterior margin of tergum 8 broadly emarginate medially.

*Discussion.*— Only a single specimen, a female, of *Neobrachida* is known. It, therefore, was not possible to do dissections required for detailed examination of many structural features. The spermatheca is visible through the sides of the abdomen, but it is not possible to determine detailed structure.

Relationships of *Neobrachida* are uncertain. The divided ligula seems to place it in the "*Sternotropa*" lineage and structure of the setal patch on tergum 10 suggests it may be related to *Sternotropa*. However, more precise relationships cannot be resolved at present (see Phylogenetic Analysis).

*Natural history.*— Unknown.

*Immature stages.*— Undescribed.

*Distribution.*— Only known specimen from Ceylon.

*Major literature.*— *Neobrachida* is only known from descriptions by Cameron (1920a, 1939).

### *Adelarthra* Cameron

Figs. 53, 93, 114, 212, 230, 231

*Adelarthra* Cameron 1920b:222. Type species: *Adelarthra barbari* Cameron 1920b:222. Fixed by Cameron 1920b:222 by monotypy.

*Diagnostic combination.*— Small beetles (adults 1.1 to 1.2 mm in length); body form slightly limuloid, broadest near middle of elytra, sides convergent posteriorly to apex of pointed abdomen; moderately robust; sculpture smooth throughout, integument shining; microsetae small, scattered, body subglabrous; macrosetae on lateral margins of pronotum, elytra, and abdomen extremely large, dark, bristle-like. Pronotum markedly transverse, 1.9 times as wide as long; convex, sides moderately depressed, antero-lateral angles markedly depressed;

hypomera not visible in lateral aspect; posterior margins moderately bisinuate. Elytral apico-lateral angles sinuate. Mesosternum with slight medial longitudinal carina. Meso- and metasternal processes broad between coxae; suture between processes fused, indistinguishable. Labium with ligula bifid to base, lobes robust, parallel-sided, rounded apically.

**Description.**— Adult length 1.1 to 1.2 mm. Body sublimuloid, broadest near middle of elytra, broadly rounded anteriorly to head, sides convergent posteriorly to apex of pointed abdomen; moderately robust; sculpture smooth throughout, integuments shining; microsetae small, widely scattered, much of body glabrous, punctures very fine; macrosetae various on different regions of body: small and inconspicuous, or very long, dark and conspicuous.

**Head.** Markedly transverse; microsetae very few, small, widely scattered, punctures minute; macrosetae absent. Eyes moderate in size. Infraorbital carina moderately developed, complete ventrally. Neck carina present, more or less slight, obsolete ventrally. Antenna with antennomere 4 similar in setation and general shape to 1-3; antennomeres 4-10 slightly transverse, similar in width.

**Mouthparts.** Labrum (Figure 53) with major setae well developed, without accessory setae; lateral sensilla row with three to five small spine-like sensilla, distant from lateral margin; sensilla of medial sensory area well developed. Mandibles not bifid at apex; right mandible with small internal tooth; prostheca typical of subtribe. Maxilla (Figure 93) with apex of lacinia truncate, with well developed "spore brush"; teeth numerous, small and closely spaced; inner face of lacinia with single row of setae, galea with apical setae in four distinct rows, setae flattened. Labium (Figure 114) with ligula bifid to base; lobes robust, parallel-sided, rounded apically; single medial seta.

**Thorax.** Pronotum (Figure 231) markedly transverse, 1.9 times as wide as long; moderately convex in cross-section; broadest at base, broadly rounded and convergent to anterior angles; sides moderately depressed; antero-lateral angles markedly depressed; hypomera not visible in lateral view; anterior margin and antero-lateral angles broadly rounded; posterior margin bisinuate, not emarginate medially; microsetae absent; macrosetae very small, inconspicuous or obsolete, except L3 prominent. Elytra (Figure 231) transverse, broader at base than pronotum, sutural length equal to pronotal length; elytra shorter at suture than laterally; apico-lateral angles moderately sinuate; microsetae very small, very sparsely and uniformly distributed; macrosetae on lateral margins extremely large, dark and prominent. Prosternum markedly transverse, with transverse carina, carina more prominent, ridge-like medially; medially with marked transverse tooth. Mesosternum with narrow but distinct medial longitudinal carina. Meso- and metasternal processes extended broadly between middle coxal cavities; suture fused, processes indistinguishable. Middle coxal cavities widely separated. Metepisternum bare. Tarsomere 1 of hind tarsus as long as next two together.

**Abdomen** (Figure 231). Robust, sides convergent from base to slightly pointed apex. Terga 3-6 moderately to slightly transversely impressed. Microsetae few; macrosetae very large, dark, bristle-like. Microsculpture of fine ridges divergent proximally from each setal insertion. Tergum 10 with medial setose patch more or less square, setae few, unmodified. Sterna unmodified.

**Aedeagus** (Figures 212, 230). Similar to that found among specimens of *Sternotropa* and *Pseudoligota*.

**Spermatheca.** Unknown.

**Secondary sexual characteristics.** Absent.

**Discussion.**— Because of the large dark bristles on the body and the robust sublimuloid body form of members of *Adelarthra*, this is one of the most distinctive taxa among gyrophaenines.

Relationships of *Adelarthra* are uncertain. Similarities in the aedeagus to members of *Sternotropa* and *Pseudoligota* indicate that it shares affinities with these taxa (see Phylogenetic Analysis for detailed discussion).

**Natural history.**— Not known. Specimens have been collected from rotten wood and "debris" (label data).

**Immature stages.**— Not described.

**Distribution.**— The two known specimens are from Singapore.

**Major literature.**— Discussed only in original description.

### *Brachychara* Sharp

Figs. 19, 54, 71, 94, 116, 129, 174, 189, 213, 232, 237, 243, 249, 250

*Brachychara* Sharp 1883:267. Type species: *Brachychara crassa* Sharp 1883:267. Fixed by Fenyes 1918-21:21 by subsequent designation. —Fenyes 1918-21:94. —Cameron 1922:637.

**Diagnostic combination.**— Adults 1.8 to 3.0 mm in length. Body form sublimuloid, markedly robust; body moderately to slightly pubescent; microsetae short, stiff, uniformly

distributed; integument shining. Pronotum moderately transverse, 1.5 to 1.8 times as wide as long; very markedly convex, lateral margins markedly deflexed; antero-lateral margins deflexed to vertical; hypomera not visible in lateral aspect; posterior margins bisinuate. Elytral apico-lateral angles markedly sinuate. Mesosternum with slight broad medial longitudinal ridge. Mesosternal process extended to middle or slightly posterior to middle of mid-coxal cavities; suture between meso- and metasternal processes fused. Maxilla with setae on inner face of lacinia scattered; setae on apex of galea in four widely separated rows, setae flattened, subspatulate. Labium with ligula bifid to base; lobes broadly separate at base, pointed apically.

*Description*.— Adult length 1.8 to 3.0 mm. Body shape sublimuloid, very robust, broadly oval in cross section. Body markedly shining, moderately to slightly pubescent, pubescence stiff, scattered.

*Head* (Figure 54). Transverse, oval, deflexed to more or less vertical plane; base hidden in dorsal aspect by anterior margin of pronotum. Shining, without sculpture; moderately pubescent, microsetae short, stiff, widely scattered; punctures small; macrosetae absent. Eyes moderate in size. Infraorbital carina well developed, complete. Neck carina well developed. Antenna various; antennomere 4 similar in setation and general shape to 1-3.

*Mouthparts*. Labrum (Figure 54) with major setae well developed; with few scattered accessory setae; lateral sensilla row of four or five spine-like sensilla, near lateral margin; slightly sclerotized along midline. Mandibles (Figure 71) not bifid at apex; right mandible with small internal tooth. Prostheca typical of subtribe. Maxilla (Figure 94) with apex of lacinia truncate, very broad, with extensive area of very numerous, small, closely spaced teeth; inner face of lacinia with setae small, numerous, scattered; galea with apical setae in three distinct and one indistinct (most proximal) rows, rows long, crowded near apex, setae spatulate to plate-like. Labium (Figure 116) with ligula bifid to base; the two lobes widely separated at base, acutely pointed apically; single medial seta.

*Thorax*. Prothorax (Figure 129) markedly transverse, 1.5 to 1.8 times as wide as long; very markedly convex in cross-section, sides markedly depressed, antero-lateral margins depressed to vertical; hypomera not visible in lateral view; anterior margin broadly rounded; hind margins moderately to markedly bisinuate, not emarginate medially; sculpture absent, integument shining; microsetae short, depressed, widely scattered, more or less uniformly distributed; punctures small; macrosetae very small, inconspicuous. Elytra short, each elytron shorter than wide, longer laterally than at suture; apico-lateral angles markedly sinuate; surface markedly shining; reticulate ground sculpture absent but specimens of some species with punctures united by very fine raised lines; uniformly covered with short appressed microsetae; macrosetae small. Prosternum very short in front of coxae; transverse; with distinct transverse medial knob or protuberance. Mesosternum short, markedly upturned on anterior edge; longitudinal carina absent; medially with slight, broad, longitudinal ridge extended almost to apex of mesosternal process. Mesosternal process extended to just posterior to middle of midcoxal cavities. Metasternal process broadly rounded; suture between meso- and metasternal processes fused, slightly raised as low bead along fusion line. Coxae widely separated (Figure 250). Metepisternum (Figure 249) with setae numerous, in two or three very irregular rows; setose area not delimited by a carina. Tarsomere 1 of hind tarsus as long as next two together.

*Abdomen*. Robust, broadly oval in cross section; sides convergent from broad base to narrow apex. Terga 3-5 or 3-6 very slightly transversely impressed. Sterna unmodified. Tergum 7 with anterior margin modified as opening of abdominal gland ducts. Tergum 10 (Figure 174) with medial setose patch chevron-shaped, setae in three distinct rows; setae flattened, subspatulate.

*Aedeagus* (Figure 213). Apical lobe of median lobe elongate, spine-like; flagellum long, slender, whip-like, coiled apically.

*Spermatheca* (Figure 189). Typical of subtribe; simple.

*Secondary sexual characteristics*. Tergum 8 of both male and female modified. Female with tergum 8 broadly incised medially, each lateral edge of incision extended posteriorly as slight spine; emargination medially with or without broad slight lobe; Male with tergum 8 deeply emarginate, each lateral edge prolonged as large inwardly curved spine; emargination with large, more or less pointed lobe medially.

*Discussion*.— The very robust, convex, sublimuloid body form, shining integuments, and very extensive “spore brush” of numerous, short, densely arranged teeth make this one of the most distinctive gyrophaenine genera.

Sharp (1883) stated that *Brachychara* was “best located near *Brachida*”, but he did not believe that these two taxa were closely related. It appears that *Brachychara* is most closely related to *Agaricomorpha* new genus, and together they form a monophyletic lineage (see Phylogenetic Analysis).

*Natural history*.— Members of *Brachychara* are most common on fleshy or leathery polypores on logs. Both larvae and adults have been found on mushrooms of this type (personal observations, and label data).

*Immature stages*.— Not described.

*Distribution*.— Species of *Brachychara* are known from Central America and St. Vincent in the West Indies. There are a number of undescribed species in Mexico and Central America.

*Major literature*.— Known only from original descriptions. Comprehensive keys and illustrations of structural features have not been previously published.

*Agaricomorpha* new genus

Figs. 20, 28, 55, 72, 95, 117, 130, 140, 148, 155, 160, 175, 190, 214, 215, 236, 242, 244, 248

*Agaricomorpha* new genus. Type species: *Agaricomorpha apacheana* (Seevers) 1951:743 (from *Gyrophaena* (*Agaricochara*)). Fixed here by original designation.

*Diagnostic combination*.— Small beetles (adults 1.0 to 1.6 mm in length). Body more or less flattened to slightly convex; broadest near middle of elytra, sides of abdomen convergent from base to more or less obtusely pointed apex. Head transverse (1.2 to 1.4 times as wide as long); slightly to moderately deflexed, oblique. Pronotum markedly transverse, 1.8 to 2.1 times as wide as long; slightly convex in cross section; lateral margins deflexed, hypomera not visible in lateral aspect; posterior margins moderately to markedly bisinuate, not emarginate medially. Mesosternum with complete, incomplete or without medial longitudinal carina. Mesosternal process extended to slightly posterior to middle, or to posterior 2/3 of mid-coxae; meso- and metasternal processes in contact along broad, truncate suture, or suture fused, processes indistinguishable. Maxilla with setae on inner face of lacinia in single row or scattered; setae on apex of galea in four distinct rows, setae flattened, subspatulate. Labium with ligula protruded, parallel-sided, bifid 2/3 to 3/4 distance to base; single medial seta. Aedeagal form distinctive (Figures 214, 215), median lobe with apical process lateral to origin of flagellum.

*Description*.— Length of adults 1.0 to 1.6 mm. Body more or less flattened to slightly convex; broadest near middle of elytra, abdomen convergent to more or less obtusely pointed apex; sculpture reticulate throughout, integuments subshining to dull; microsetae short, more or less densely arranged throughout; punctures small, asperate in many; macrosetae small, difficult to distinguish from microsetae.

*Head* (Figure 20). Transverse (1.2 to 1.4 times wider than long); slightly to moderately deflexed to oblique plane; tempora short, rounded to acutely convergent to base of head; microsetae numerous, short, more or less densely and uniformly distributed; macrosetae absent. Eyes moderate in size. Infraorbital carina well developed, or slightly developed antero-ventrally. Neck carina slightly developed. Antenna (Figure 28) longer than head and thorax together; antennomere 4 similar in setation and general shape to 1-3, subquadrate to slightly elongate; 5-7 longer than wide, 8-10 subquadrate, quadrate, or slightly transverse.

*Mouthparts*. Labrum (Figure 55) with major setae well developed, without accessory setae; lateral sensilla row with two to five moderately developed spine-like sensilla, distant from or near lateral margin; sensilla of medial sensory area well developed. Mandibles (Figure 72) not bifid at apex; right with small internal tooth; prosthema typical of subtribe. Maxilla (Figure 95) with apex of lacinia obliquely truncate, with well developed "spore brush"; teeth of spore brush small, close, densely arranged; setae on inner face of lacinia more or less numerous to few, scattered or in single well developed row; galea with apical setae in four distinct, clearly separated rows, setae flattened, subspatulate. Labium (Figure 117) with ligula protruded, parallel-sided, bifid 2/3 to 3/4 distance to base; single medial seta.

*Thorax*. Prothorax (Figure 130) transverse to markedly transverse (1.8 to 2.1 times as wide as long); slightly convex in cross-section; lateral margins moderately deflexed, hypomera not visible in lateral aspect; posterior margin moderately to markedly bisinuate, not emarginate medially; microsetae small, numerous, densely and uniformly distributed; macrosetae very small, inconspicuous. Elytral apico-lateral angles moderately to markedly sinuate. Prosternum (Figure 148) transverse, with medial knob, carina or protuberance. Mesosternum with medial longitudinal carina, complete, obsolete or absent in posterior 1/2, or absent. Mesosternal process extended to slightly posterior of middle of, to posterior 2/3 of middle coxal cavities. Suture between meso- and metasternal processes complete, unmodified, or fused, processes indistinguishable (Figure 155). Metepisternum (Figures 160, 248) with setae in one or two irregular rows, setose area margined antero-ventrally by slight carina or not. Tarsomere 1 of hind tarsus 1.0 to 1.3 times as long as 2; with slight ventro-lateral ctenidium of five to seven setae.

*Abdomen*. Sides convergent from base to apex. More or less pubescent, microsetae short. Terga 3-5 moderately to slightly transverse. Sterna not modified. Tergum 7 with anterior margin modified for opening to abdominal gland ducts. Tergum 10 (Figure 175) with medial setose patch chevron-shaped; setae numerous, short, slightly flattened.

*Aedeagus* (Figures 214, 215). Distinctive. Median lobe with apical process simple, more or less blade-like, lateral to origin of flagellum. Parameres various, not extremely modified.

*Spermatheca* (Figure 190). Typical of subtribe; simple.

*Secondary sexual characteristics.* Various. Most males with posterior margin of tergum 8 with broad semicircular emargination medially, lateral margins of emargination with small spine-like processes or not. Female with posterior margin of tergum 8 broadly, shallowly emarginate or not, or with margin broadly bisinuate.

*Discussion.*— The taxon *Agaricomorpha* is established here to contain the New World species of *Gyrophana* (*Agaricochara*) (*sensu* Seevers, 1951) with divided ligula. Seevers (1951) based his concept of *Agaricochara* (as a subgenus of *Gyrophana*) primarily on antennal structure, very transverse pronotum and intercoxal processes which are similar in length. He did not recognize that among those species he included in *Gyrophana* (*Agaricochara*) were some which have members with entire ligulae, and some with bifid ligulae. Those with an entire ligula should be tentatively included in *Gyrophana* until that genus has been more thoroughly studied. Among those with bifid ligula, I have argued elsewhere (see discussion under *Agaricochara* Kraatz) that the European species of *Agaricochara* form a monophyletic group. Members of the New World species with bifid ligula differ from the European *Agaricochara* in form of the median lobe of the aedeagus, and in having a more deeply bifid ligula, chevron-shaped setal patch on tergum 10, more closely joined or fused intercoxal processes, more deeply bisinuate posterior margins of pronotum and more markedly sinuate apico-lateral angles of elytra, and more transverse pronotum. The New World forms seem more closely related to *Sternotropa* and *Brachychara* than to *Agaricochara*. It therefore seems necessary that these forms be placed in a genus separate from the Old World *Agaricochara*.

*Agaricomorpha* appears to be most closely related to *Brachychara* (see Phylogenetic Analysis).

*Type species.*— *Gyrophana* (*Agaricochara*) *apacheana* Seevers 1951:743 is here designated as the type species of *Agaricomorpha* new genus. *G. apacheana* is chosen because it appears to be the first described species of this taxon. Considering the abundance and diversity of members of *Agaricomorpha* in Mexico and Central America, it is surprising that species assignable to this genus were not described by Sharp, Bernhauer or Cameron in their studies of staphylinids from these regions. However, I have had occasion to examine most of the species described by these workers and have not found any assignable to *Agaricomorpha*. The type specimen of *A. apacheana* is a male in the collection of the California Academy of Sciences.

*Included species.*— The following species is transferred from *Gyrophana* (*Agaricochara*) (*sensu* Seevers, 1951) to *Agaricomorpha* new genus:

*Agaricomorpha apacheana* (Seevers, 1951:743) new comb.

In addition, I have seen specimens of a number of undescribed species from Mexico and Central America.

*Natural history.*— Adults and larvae of *Agaricomorpha* have been found on woody and leatherly polypore mushrooms on logs, and appear to be characteristic inhabitants of these mushrooms (personal observations).

*Immature stages.*— Undescribed.

*Distribution.*— The described species of *Agaricomorpha* is found only in the southwestern United States. However, I have seen a number of undescribed species from Mexico and Central America. It seems likely that members of *Agaricomorpha* also occur in South America.

*Major literature.*— Only known from original description by Seevers (1951).



## EVOLUTIONARY ANALYSIS OF GENERA OF GYROPHAENINA

**Character Analysis**

*Methods and Principles of Character Analysis.*— The basic process in determination of relationships between taxa is analysis of characters.

Characters or attributes are features by which means taxa are identified and described. These characters also provide information about genealogical relationships. Hecht and Edwards (1977: 5) define a character as “a set of limited homologous features that are distributed among two or more taxa.” Different expressions of the character among taxa under consideration are called “character states”. The suite of character states, assumed to be homologous, is called a “morphocline” or “morphological transformation series”. In every morphological transformation series, there is a single ancestral condition, but there can be one or more derived states. Direction of change in a transformation series is called “polarity”. Polarity of a transformation series is in a uni- or multidirectional series (Hecht and Edwards, 1977).

Effective character analysis resolves into three distinct phases: 1) recognition and description of homologous character states; 2) development of hypotheses about relative usefulness of states of different characters for phylogenetic analysis (character weighting); and 3) development of hypotheses about the polarity of transformation series.

To effectively make hypotheses about relationships of taxa it is necessary to be able to compare structures which are derived from a common ancestral condition; that is, homologous character states. When features appear similar in structure and/or development but are not derived from the same common ancestor, the condition is termed homoplasy. Two types of homoplasy occur: that due to parallelism and that due to convergence. Of these, for phylogenetic analysis, parallelism is the most important, since it involved development of similar but non-homologous character states in relatively closely related lineages. Hecht and Edwards (1977) correctly state that failure to recognize parallelism is probably the most common cause of misinterpretation of phylogenetic relationships. Recognition of parallelisms is discerned not only by subtle differences in development and/or structure that indicate non-homology, but also by degree of congruence of character states in a reconstructed phylogeny under the principle of parsimony. (While there is no reason to believe that evolution produces parsimonious character state distributions, rejection of parsimony as a working principle should be done only in response to strong evidence to the contrary.) Distribution of character states in a cladogram is very sensitive to hypotheses about relative weight of characters and polarity of transformation series. Character weighting is necessary because some characters have more reliable information about phylogenetic relationships than others. That is, some characters are less likely to be derived in parallel and/or parallelisms are more easily recognized in these characters than in others. Hecht and Edwards (1977) review suggestions for weighting characters by Wilson (1965), Inger (1967), Kluge and Farris (1969) and Hecht and Edwards (1976). In general, these authors agree that characters of low weight are those which involve loss or reduction of structures, those resulting from common growth processes, and those which show great variability in other groups. I would add to these, those characters for which polarity of the transformation series is not clearly analysed. Those which should be given high weight have unusual developmental patterns, are parts of integrated complexes, or are innovative and unique for the transformation series. These criteria are generally accepted in this treatment, but evaluation of each character must be done independently.

Development of hypotheses about polarity of transformation series is fundamental to character analysis. Subsequently, the literature about methods for determination of polarity is extensive. De Jong (1980) has critically reviewed the main methods for recognition of polarity and major recent discussions are found in Hecht and Edwards (1977) and Watrous and Wheeler (1981).

Generally, determination of polarity of a transformation series requires comparison of the states of the character system both among the taxa being compared (in-group comparisons) and among closely and more distantly related taxa (out-group comparison). In the simplest instance, if two states of a character occur within a taxon, and only one is found in out-group comparison, then the more restricted state is considered the apotypic condition (Watrous and Wheeler, 1981). The polarized character can then be compared with others for congruence. In practice, more complex distributions of character states may make this much more difficult than this example would indicate (see De Jong, 1980, Watrous and Wheeler, 1981, and references included therein).

In this revision, members of the subtribe Gyrophaenina provide in-group comparisons, while members of the subtribe Bolitocharina provide out-group comparisons from a closely related group, and the aleocharines as a whole provide more distantly removed comparisons. In general, it is argued here that a character state found in the bolitocharines and some, but not all, gyrophaenines is plesiotypic.

In order to facilitate critical evaluation of the character states and hypotheses about polarity of transformation series presented here, I use the same format for discussion of each character. This includes: 1) recognized states of the character; 2) the transformation series recognized among these traits; 3) hypotheses and justification for hypotheses about plesiotypic and apotypic states; 4) specific problems associated with interpretation of individual characters plus alternative hypotheses; and 5) probable usefulness of the character in phylogenetic analysis. Character states discussed in this study are summarized in Table 1, and known distribution of these states among gyrophaenine genera is summarized in Table 2.

*Character Systems: Analysis.*— Character 1 — Body setae: microsetae. — States of this character among the gyrophaenines form a more or less continuous series, which is conveniently, though arbitrarily divided into four states: 1) setae numerous, more or less short, densely and uniformly distributed over the body (*A*); 2) setae numerous, more or less long and silky, densely and uniformly distributed (*B*); 3) setae short, number reduced, body subglabrous (*C*<sub>1</sub>); and 4) setae short, number markedly reduced, body more or less glabrous (*C*<sub>2</sub>). Of these, State *A* is considered to be plesiotypic, on the basis of out-group comparison. It characterizes specimens of most bolitocharines and many other groups of aleocharines. Two transformation series of this character are recognized: one in which short, numerous setae become long, silky setae (*A*→*B*); and one in which number and density of setae are reduced (*A*→*C*<sub>1</sub>→*C*<sub>2</sub>).

Alternative hypotheses about polarity of this character are hard to justify. State *C*<sub>1</sub> characterizes specimens of many species of *Gyrophaena* which also have a relatively large number of plesiotypic states of other characters. This state may be hypothesized to be the plesiotypic condition. However, scarcity of this state among bolitocharines argues against this. Also, this polarity would require evolution of an increased number of setae. While possible, this hypothesis seems less parsimonious than one in which reduction was more common.

Alternatively, State *B* could be considered plesiotypic. This hypothesis is given some justification by origin near the base of the cladogram of both genera whose members have this state. Absence of this state among bolitocharines, and rarity of this condition among other

aleocharines seems to argue against this.

Because the states of this character are arbitrary divisions of a continuum, it is difficult to place the condition of some specimens into one or another. Also, because one transformation series ( $A \rightarrow C_1 \rightarrow C_2$ ) is regressive, it has almost certainly occurred many times independently. Therefore, this character is unreliable for phylogenetic inference.

Character 2 — Body setae: macrosetae. — As for Character 1, the 3 states are more or less arbitrary divisions of a continuum: 1) macrosetae small, difficult to distinguish from microsetae ( $A$ ); 2) macrosetae larger, easily distinguished from microsetae ( $B_1$ ), and 3) macrosetae extremely large, very conspicuous ( $B_2$ ). Of these, State  $A$  is considered to be plesiotypic.

Justification for this polarization is weak. State  $A$  is the most common condition among bolitocharines and is also commonly found among a large number of other aleocharines. If this polarity is correct, a single transformation series of increasing size and prominence of macrosetae is produced ( $A \rightarrow B_1 \rightarrow B_2$ ). This is probably too simple and additional study would reveal a more complex set of possible character states.

Because the states are arbitrary parts of a continuum, it is often difficult to interpret. Also, some specimens show 2 or more states of macrosetae, depending on the setae considered. In addition, apotypic states have almost certainly been derived a number of times independently within the gyrophaenines. Therefore, this character is not very useful for phylogenetic analysis.

Character 3 — Sculpture. — Three states of this character are recognized: 1) body uniformly reticulate ( $A$ ); 2) body sculpture obsolete or smooth on one or more sclerites ( $B_1$ ); and 3) sculpture absent, integument uniformly smooth ( $B_2$ ). State  $A$  is considered plesiotypic. Justification of this polarity is by both out-group and in-group comparison. Most bolitocharines and many other aleocharines in many groups have reticulate integumental sculpture. Also, specimens of many species in almost all genera of gyrophaenines exhibit State  $A$ . If this polarity is correct then a single transformation series is indicated ( $A \rightarrow B_1 \rightarrow B_2$ ).

Reticulate integumental sculpture is a basic and very common type of sculpture among staphylinids. Independent evolution of this state, or reversion to a reticulate condition from smooth integument seems a less parsimonious hypothesis than independent loss of reticulate microsculpture in a number of lineages of gyrophaenines. However, reversion from apotypic to plesiotypic states must be considered possible. Character States  $A$  and  $B_2$  are precisely defined and therefore easy to interpret. However, State  $B_1$  is a conglomeration of similar types of states, each of which may have been derived independently from an  $A$ -type ancestor or from a previous, relatively more plesiotypic  $B_1$ -type ancestor.

Because of the above problems, and because apotypic states are regressive, this character is not reliable for phylogenetic inference.

Character 4 — Head: medial macrosetae. — Two states are known: 1) a pair of macrosetae medially on vertex ( $A$ ), and 2) macrosetae absent from vertex ( $B$ ). State  $A$  is considered to be plesiotypic, based solely on in-group comparison. Similar macrosetae are not known among bolitocharines, or, to my knowledge, among other aleocharines. Among gyrophaenines, there are macrosetae on the vertex in most members of *Brachida* and specimens of a very few species of *Gyrophaena* and *Eumicrota*. This distribution suggests that such macrosetae were present in ancestral gyrophaenines, and these have subsequently been lost from most lineages.

The alternative hypothesis, that macrosetae on the vertex are derived within gyrophaenines is possible. However, the uniform position of these macrosetae, and the phylogenetically disjunct distribution of such macrosetae do not support this hypothesis. The possibility that presence of macrosetae may be apotypic for the Gyrophaenina as a whole is given support by

absence of such setae from out-groups. This distribution may be a result of inadequate survey of this character within these groups. Even so, the polarity of the transformation series given above ( $A \rightarrow B$ ) remains correct within the context of the gyrophaenines.

Because apotypic states of this character are regressive and loss of macrosetae may have occurred numerous times within the gyrophaenines, this character is of little use for phylogenetic inference.

Character 5 — Infraorbital carina. — Two states are recognized: 1) infraorbital carina well developed, complete ventrally ( $A$ ), and 2) infraorbital carina incomplete, reduced or absent ventrally ( $B$ ). Of these, State  $A$  is considered plesiotypic. Justification for this hypothesis is well established from both out-group and in-group comparison. An infraorbital carina is well developed among most bolitocharines, many other aleocharines and most gyrophaenines.

Because apotypic states are regressive, it has very limited use in phylogenetic inference.

Character 6 — Head: lateral macrosetae. — Two states known: 1) macrosetae (other than a medial pair in specimens of a few species) absent from the dorsal surface of the head ( $A$ ), and 2) two macrosetae on dorsal surface of the head on each side, medial to the anterior and posterior margin of the eye ( $B$ ). Based on both in-group and out-group comparison, State  $A$  is considered plesiotypic. Macrosetae in this position are unknown among bolitocharines and most gyrophaenines. Among gyrophaenines, such macrosetae are known only in the subgenus *Acanthophaena* of *Phanerota* and are probably uniquely derived within the subgenus.

Because of the limited distribution of apotypic states of this character, it is not useful for phylogenetic inference at the generic level. However, it does provide evidence that the subgenus *Acanthophaena* is a monophyletic assemblage.

Character 7 — Eyes. — Two states are recognized: 1) eyes moderate in size ( $A$ ), and 2) eyes extremely large, prominent ( $B$ ). Based on both in-group and out-group comparison, State  $B$  is considered apotypic. Very large eyes are not found among bolitocharines, most other aleocharines, or among most gyrophaenines. Among gyrophaenines, extremely large eyes are found among members of the genus *Phanerota* and are probably uniquely derived within that genus.

Because of the limited distribution of this character within gyrophaenines, it is not useful for intergeneric phylogenetic inference. However, it provides strong evidence that *Phanerota* is a monophyletic assemblage.

Character 8 — Antenna: antennomere 4. — Two states are recognized: 1) antennomere 4 similar in setation and general shape to antennomeres 5-10 ( $A$ ), and 2) antennomere 4 similar in setation and general shape to antennomeres 1-3 ( $B$ ). Of these, State  $A$  is considered plesiotypic, based on out-group comparison. Most bolitocharines and many other aleocharines exhibit the plesiotypic condition.

Although in words, the states of this condition appear ambiguous, it is, in fact, within gyrophaenines, seldom difficult to assign an observed condition to one or the other states. Intermediate conditions are found only among some members of *Brachida*. Modification of antennomere 4 to a general form different from antennomeres 5-10 gives the antennae of those gyrophaenines possessing the apotypic condition a distinctive appearance.

Though conditions similar to State  $B$  may have evolved numerous times among other aleocharines, there seems little justification for the hypothesis that State  $B$  is plesiotypic among gyrophaenines.

This character seems fairly useful for phylogenetic inference within the gyrophaenines.

Character 9 — Labrum: number of setae. — Two states are recognized: 1) labrum with numerous setae in addition to the basic setal pattern (*A*) (see section about structural features for description), and 2) labrum with few or no setae other than those in the basic pattern (*B*). Of these, State *A* is considered plesiotypic. Justification for this hypothesis is from both in-group and out-group comparisons. Some bolitocharines and many other aleocharines have numerous setae on the labrum. Among the gyrophaenines, State *A* is found among those groups which also exhibit other characters on the labrum believed to be plesiotypic.

It is important to note that many bolitocharines and also many other aleocharines exhibit conditions similar to State *B*. This provides some justification for the alternative hypothesis that State *B* is the plesiotypic condition. This is undeniably possible, but the association of State *A* with other presumed plesiotypic character states in the labrum of gyrophaenines, while weak evidence, is suggestive that state *A* is plesiotypic. Also, acceptance of State *B* as plesiotypic would require that apotypic states involve a gain rather than a loss. Without at least rudimentary evidence to the contrary, it seems more parsimonious to postulate a loss rather than a gain. Therefore, the hypothesis that State *A* is plesiotypic within the gyrophaenines seems to be the most parsimonious hypothesis. This implies that conditions similar to State *B* among other aleocharines are the result of independent evolution of this state, perhaps numerous times.

This character has limited use for phylogenetic inference among gyrophaenines. However, because of the relatively weak justification for character polarity and because the regressive nature of the apotypic states suggests the possibility that this state may have arisen several times independently within the gyrophaenines, this character must be used with caution.

Character 10 — Labrum:  $\alpha$ -sensillum. — Two states of this character are recognized: 1)  $\alpha$ -sensillum filiform, seta-like (*A*), and 2)  $\alpha$ -sensillum thickened, hyaline. State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Most bolitocharines, many other aleocharines and most gyrophaenines exhibit State *A*.

Apotypic states are uncommon and erratically distributed among several genera of gyrophaenines. The apotypic condition has probably been derived independently a number of times in one or more lineages within several genera. Therefore, this character is not useful for phylogenetic analysis at the level considered here.

Character 11 —  $\epsilon$ -sensillum. — Three states are recognized: 1)  $\epsilon$ -sensillum large, indistinguishable from labral setae (*A*); 2)  $\epsilon$ -sensillum setose, but much smaller than labral setae (*B*<sub>1</sub>); and 3)  $\epsilon$ -sensillum reduced to a small peg-like object (*B*<sub>2</sub>). Of these, State *A* is considered plesiotypic, based on occurrence of State *A* in association with other plesiotypic conditions in both gyrophaenines and other aleocharines.

If this polarity is correct, then a single transformation series based on progressive reductions of the  $\epsilon$ -sensillum can be recognized (*A*→*B*<sub>1</sub>→*B*<sub>2</sub>).

Justification for the hypothesis that State *A* is plesiotypic is not strong. However, the alternative hypothesis, that State *B*<sub>2</sub> is plesiotypic and more apotypic states of this character result in more seta-like  $\epsilon$ -sensilla, does not seem to be suggested by either in-group or out-group comparison.

Weak justification of polarity and the fact that apotypic states of this transformation series involve regression suggests that this character has limited value for phylogenetic inference.

Character 12 — Labrum: position of lateral sensilla row. — Two states are recognized: 1) sensilla of row near or at lateral margin of labrum (*A*), and 2) sensilla of row more or less distant from lateral margin (*B*). Of these, State *A* is considered plesiotypic. Justification for

this hypothesis is from both in-group and out-group comparison. Among gyrophaenines, State *A* occurs among species which arise early in the cladogram, and in association with other presumed plesiotypic labral conditions. State *A* is also found among many bolitocharines.

Since State *B* also occurs in other aleocharines, it is possible that this is the plesiotypic condition. However, in-group comparisons among the gyrophaenines do not support this.

Weak justification of the polarity of this transformation series suggests that the value of this character for phylogenetic inference is uncertain.

Character 13 — Labrum: development of lateral sensilla row. — Two states are recognized: 1) four or five well developed sensilla in row (*A*), or 2) number and development of sensilla less (*B*). Based on both in-group and out-group comparison, State *A* is considered plesiotypic. State *A* is the most common condition among gyrophaenines and occurs in specimens of at least some species in all genera. Also, among gyrophaenines, State *A* occurs in all species of groups placed near the beginning of the cladogram and in association with other presumed plesiotypic states in the labrum of these species. In addition, many bolitocharines and many other aleocharines have State *A*.

The wide distribution of the plesiotypic condition among gyrophaenines makes this character of limited use for phylogenetic inference at the generic level.

Character 14 — Labrum: position of A.L.1 and A.L.2. — Two states are recognized: 1) origin of A.L.1 and A.L.2 more or less distant from the margin of the labrum (*A*), and 2) origin of A.L.1 and A.L.2 at the margin of the labrum (*B*). State *A* is considered plesiotypic, with reservations, based on both in-group and out-group comparison. Among gyrophaenines State *A* occurs in association with other presumed plesiotypic conditions. Also, State *A* occurs in specimens of some species in most genera. In addition, most bolitocharines have State *A*. These justifications are weakened by the wide distribution of State *B* among gyrophaenines, bolitocharines and other aleocharines.

While the condition of this character in most specimens is relatively easy to assign to one or the other of these states, in specimens of some species, intermediate conditions exist (e.g. one seta of pair near and one distant from labral margin (Figure 50)), which makes this character difficult to use in practice.

Weak justification for polarity of the transformation series, intermediate states, and probable multiple derivation of the presumed apotypic condition suggest that this character has little use in phylogenetic inference at the present time.

Character 15 — Labrum: internal setose areas. — Two states are recognized: 1) densely setose area present internally on each side of labrum (*A*), and 2) densely setose area absent internally on each side of midline (*B*). The polarity of this transformation series is not clear. Presence of State *A* only among species which arise near the base of the cladogram, and association with other labral character states presumed to be plesiotypic, suggest that this state is plesiotypic among the gyrophaenines. This hypothesis is given some support by the fact that State *A* occurs in some, but not all, species in both *Probrachida* and *Brachida*. If this hypothesis is correct then State *B* would have been independently derived by species within each of these genera, and also all remaining gyrophaenines.

The alternative hypothesis, that State *B* is plesiotypic, is supported by the fact that I have not observed State *A* among the bolitocharines that I have examined, and the distribution of State *A* is unknown among other aleocharines. This suggests that State *A* may be derived within the lineages which lead to *Probrachida* and *Brachida*. Because it is not clear whether these two genera are derived from a common ancestor (see below for details), it is uncertain

whether this character must have been derived once or twice within the gyrophaenines. However, in either instance, if State *A* is a derived condition in the ancestor(s) of the two lineages of gyrophaenines in which it occurs, then other species in each lineage must have reverted to the plesiotypic condition independently.

I am unable to favor one of these two alternatives over the other. The hypothesis that State *A* is plesiotypic is the most parsimonious, but is not supported by out-group comparison. In contrast, the hypothesis that State *B* is plesiotypic is supported by limited out-group comparisons, but is less parsimonious because it requires assumption of regression to a plesiotypic state in at least some species. A more thorough study of this character within both bolitocharines and other aleocharines would probably allow one to choose between these hypotheses.

Because of the uncertainty of polarity of the transformation series of this character, it is not useful for phylogenetic inference.

Character 16 — Mandibles: form of apex. — Three states of this character are recognized: 1) neither mandible bifid at apex (*A*); 2) left mandible bifid at apex (*B*); and 3) both mandibles bifid at apex (*C*). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. State *A* is distributed among most gyrophaenines. State *B* is characteristic of specimens of most species of *Brachida*, while States *A*, *B* and *C* are all distributed within the genus *Probrachida*. It is not clear whether two transformation series (*A*→*B* and *A*→*C*) are represented by these states, or only a single series (*A*→*B*→*C*). This is an important consideration, since if only one transformation series is represented, it implies the possibility of a sister group relationship between *Probrachida* and *Brachida*. If, on the other hand, two series are involved, then the evidence for a sister group relationship between members of these two genera is weaker. The problem is in presence of all three states among members of *Probrachida*. This implies either independent derivation of bifid mandibles, or reversion to a plesiotypic condition.

Character 17 — Mandibles: internal tooth. — Three states of this character are recognized: 1) right mandible with a well developed internal tooth (*A*); 2) mandibles without an internal tooth (*B*); and 3) both mandibles with a well developed internal tooth (*C*). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Presence of an internal tooth is widely distributed among bolitocharines, other aleocharines and gyrophaenines. Two transformation series among gyrophaenines are indicated. Absence of an internal tooth on the right mandible is considered a loss (*A*→*B*), while presence of an internal tooth on the left mandible is considered a gain (*A*→*C*).

Because the first transformation series is regressive, and distribution of the second very limited, this character has limited application for phylogenetic inference among gyrophaenine genera.

Character 18 — Lacinia: form of apex. — Two states of this character are recognized: 1) apex of lacinia more or less acute (*A*), and 2) apex of lacinia obliquely truncate (*B*). Because State *A* characterizes almost all aleocharines except gyrophaenines, this state is considered plesiotypic. All members of the subtribe Gyrophaenina have State *B* and it is considered to be uniquely derived within this group. The obliquely truncate form of the apex of the lacinia of gyrophaenines is actually one of a set of highly integrated characters which, in combination, are associated with the feeding behavior of these beetles (see Evolutionary Trends).

Since all gyrophaenines have the apotypic state for this character, it is not useful for phylogenetic inference within the group. However, it does provide evidence that the

gyrophaenines are monophyletic.

Character 19 — Lacinia: apical teeth. — Two states are recognized: 1) teeth on apex of lacinia relatively few, in, at most, a loosely defined patch, slightly, or not at all differentiated from the lateral teeth or spines (*A*), and 2) teeth on apex of lacinia numerous, closely spaced, in a well defined patch, well differentiated from the lateral teeth and spines (*B*). State *A* is considered plesiotypic, based on out-group comparison. All bolitocharines and many other aleocharines have State *A*. In addition, among those aleocharines for which mouthpart structure is accurately known, only gyrophaenines have State *B*.

State *B* is considered a uniquely derived condition within Gyrophaenina, and, as such, provides evidence that the assemblage is monophyletic.

State *B* of this character is part of an integrated complex of characters including State *B* of Character system 18 (see above).

Character 20 — Lacinia: teeth on inner face. — Three states are recognized: 1) numerous, dense, often spine-like, teeth on inner face of lacinia (*A*); 2) few, more or less scattered, teeth on inner face of lacinia (*B*<sub>1</sub>); and 3) inner face of lacinia without teeth (*B*<sub>2</sub>). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Members of *Probrachida* have State *B*<sub>1</sub> of this character in association with states of other characters which are almost certainly plesiotypic in relation to the remaining gyrophaenines. All other gyrophaenines have State *B*<sub>2</sub> of this character. State *A* is found among all bolitocharines and many other aleocharines.

States are apparently all part of a single transformation series (*A*→*B*<sub>1</sub>→*B*<sub>2</sub>). Thus, State *B*<sub>1</sub> is intermediate between numerous teeth of bolitocharines and complete absence of teeth from all other gyrophaenines. Therefore, State *B*<sub>1</sub> is plesiotypic in relation to State *B*<sub>2</sub> within the context of the Gyrophaenina.

This character is very useful for phylogenetic inference at supergeneric levels within Gyrophaenina.

Character 21 — Lacinia: setae on inner face. — Three states are recognized: 1) setae on inner face of lacinia very numerous, densely and irregularly scattered (*A*); 2) setae less numerous, few to many, more or less loosely and irregularly scattered (*B*<sub>1</sub>); and 3) setae on inner face of lacinia few to many, in a well differentiated vertical row (*B*<sub>2</sub>). State *A* is considered plesiotypic, based on both in-group and out-group comparisons. State *A* occurs in all bolitocharines and many other aleocharines. State *B* characterizes specimens of a number of groups of gyrophaenines. In specimens of *Probrachida* and *Brachida*, State *B* is found in association with other characters of the maxillae which are probably primitive. Most gyrophaenines have State *B*<sub>2</sub>.

It seems most likely that a single transformation series is represented by the states of this character (*A*→*B*<sub>1</sub>→*B*<sub>2</sub>). In contrast, it is possible that among the states characterizing gyrophaenines, State *B*<sub>1</sub> is not the direct precursor of *B*<sub>2</sub>. However, presence of both States *A* and *B*<sub>1</sub> among species of *Probrachida* and *Brachida*, and States *B*<sub>1</sub> and *B*<sub>2</sub> among species of *Agaricomorpha* and *Sternotropa* suggest that the first hypothesis (*A*→*B*<sub>1</sub>→*B*<sub>2</sub>) is most likely correct.

Although apotypic states are apparently subject to independent derivation within the gyrophaenines, when considered with other characters, this one is useful for phylogenetic analysis.

Character 22 — Galea: arrangement of apical setae. — Three states are recognized: 1) setae numerous, in close, numerous (eight to 10) rows (*A*); 2) setae numerous, rows fewer



(five to eight), but close ( $B_1$ ); and 3) setae less numerous, in four well separated rows ( $B_2$ ). Of these, State  $A$  is plesiotypic, based on both in-group and out-group comparison. State  $A$  characterizes most bolitocharines, many other aleocharines, and some members of *Brachida* among gyrophaenines. Among gyrophaenines, State  $B_1$  occurs in members of both *Probrachida* and *Brachida*. All other gyrophaenines have State  $B_2$ .

Since, among gyrophaenines, States  $A$  and  $B_1$  are associated with states of other characters of the maxillae believed to be plesiotypic, and State  $A$  is widely distributed in the out-group, a single transformation series is suggested ( $A \rightarrow B_1 \rightarrow B_2$ ).

Although apotypic states are regressive, the end point of the reduction in number of rows of galeal setae is not simply a series of variously reduced states. Instead, among gyrophaenines at least, the end point of this reduction is uniformly constant in expression as four distinct, widely spaced rows of setae. In addition, the end point of this transformation series (State  $B_2$ ) is found, with little modification, among members of many lineages of gyrophaenines. Therefore, although the apotypic states are regressive, the uniformity of the end of the transformation series suggests that it has been derived only once. Therefore, this character appears to be very useful for phylogenetic inference.

Character 23 — Galea: structure of apical setae. — Two states are recognized: 1) setae on apex of galea long, filiform, setose ( $A$ ), and 2) setae on apex of galea flattened, subspatulate or plate-like ( $B$ ). Based on both in-group and out-group comparison, State  $A$  is considered plesiotypic. State  $A$  characterizes most bolitocharines and most other aleocharines. In addition, among gyrophaenines, State  $A$  is found in members of *Probrachida* and in members of some species of *Brachida*. All other gyrophaenines have State  $B$  of this character.

Presence of both States  $A$  and  $B$  among species of *Brachida*, and State  $B$  among specimens of some species of bolitocharines suggest that the derived state of this character may be part of a functional complex related to fungus feeding. It could therefore have been derived any number of times independently in response to mushroom feeding. However, because of the invariance of State  $B$  in all gyrophaenines except *Probrachida* and *Brachida*, and uniform association of State  $B$  with the apotypic state of Character 22, it seems most parsimonious to consider State  $B$  to be of monophyletic origin in all those gyrophaenines in which it occurs except *Brachida*. This character is therefore very useful for phylogenetic inference.

Character 24 — Labium: form of ligula. — Six states are recognized: 1) ligula elongate, bifid at apex ( $A$ ); 2) ligula short, entire, protruding and parallel sided ( $B$ ); 3) ligula short, entire, broadly rounded ( $C$ ); 4) ligula short, protruding, parallel sided, divided 1/2 to 2/3 distance to bases into two more or less sharply pointed lobes ( $D_1$ ); 5) ligula short, protruding, parallel sided, divided almost or fully to base into two pointed or acutely rounded lobes ( $D_2$ ); and 6) ligula elongate, parallel sided, anterior 1/3 divided into two divergent lobes ( $E$ ). Of these, State  $A$  is the inferred ancestral condition for gyrophaenines. This condition of the ligula is not presently known in any gyrophaenine. It is instead inferred as ancestral because it is very similar to the condition found among bolitocharines and many other aleocharines. Condition of the ligula in bolitocharines (Figure 118) is probably similar to that of the common ancestor of the bolitocharines and gyrophaenines (based on additional out-group comparisons with the remainder of the Aleocharinae). It is, therefore, most parsimonious to hypothesize that the ancestor of the gyrophaenines possessed a ligula more similar to that of bolitocharines than to that represented in any extant gyrophaenine. No attempt has been made to arrange the other states of this character in a single transformation series (except  $D_1$  and  $D_2$ ). This is because I do not have evidence which allows defensible hypotheses about which, if any, of the known states

of the ligula in gyrophaenines is plesiotypic, or even which is most similar to the type from which all known types are derived. It seems, based on simplicity of structure, that two hypotheses could be considered. First, State *C*, characteristic of members of *Probrachida*, *Brachida*, and *Encephalus*, might be plesiotypic. This is suggested by occurrence of this state among species of *Probrachida* and *Brachida* placed near the base of the cladogram and possessing a large suite of other plesiotypic character states. However, it seems difficult to imagine how States  $D_1$ ,  $D_2$  and *E* could have been derived from this character state. Alternatively, State *B*, characteristic of members of *Gyrophaena*, *Phanerota* and *Eumicrota* could be similar to the ancestral condition. It seems that a condition of the ligula similar to this could easily be modified to all conditions known within gyrophaenines. However, State *B* is limited to a single lineage. If similar to the primitive condition, it might be expected to occur in more or less unmodified form in other lineages of gyrophaenines.

In addition, both these hypotheses suffer from the facts that neither occurs among bolitocharines, and both are uncommon among other aleocharines.

It therefore seems most parsimonious to recognize the following transformation series among these character states:  $A \rightarrow B$ ,  $A \rightarrow C$ ,  $A \rightarrow D_1 \rightarrow D_2$ ,  $A \rightarrow E(?)$ . The last,  $A \rightarrow E$ , is very uncertain because placement of *Neobrachida*, specimens of which have State *E*, is inadequately established. Based on a tentative placement of *Neobrachida* near *Sternotropa* (see Phylogenetic Analysis), a more reasonable transformation series would be  $D_1 \rightarrow E$ .

The most reasonable alternative to the series presented above would be:  $A \rightarrow B$ ,  $B \rightarrow C$ ,  $B \rightarrow D_1 \rightarrow D_2$  (*E* as above), based on the assumption that State *B* is plesiotypic within the gyrophaenines. As noted above, this hypothesis cannot be adequately supported.

Whether one considers each of State *B* through *E* to be apotypic within the context of gyrophaenines, or whether one considers State *B* to be plesiotypic, does not affect the structure of sister group relationships in the phylogeny. However, it does affect the way that condition of the ligula as a character supports those relationships (see discussion in Phylogenetic Analysis).

In spite of the problems outlined above, the inferences that all of States *B* to *E* of this character are apotypic in relation to that found in the ancestor of the gyrophaenines, and that States *C* and *D* are independently derived states within the gyrophaenines, seem well supported. Therefore, with the additional reservations discussed in the Structural Features section, this character is very useful for phylogenetic inference.

Character 25 — Labium: number of medial setae. — Three states are recognized: 1) two medial setae present (*A*); 2) one medial seta present ( $B_1$ ); and 3) medial setae absent ( $B_2$ ). Of these states, *A* is considered plesiotypic, based on both in-group and out-group comparisons. Most bolitocharines, most aleocharines, and, among gyrophaenines, members of *Probrachida*, have two medial setae. As far as is known all other gyrophaenines have State  $B_1$  except for a few members of the genera *Sternotropa*, *Gyrophaena* and *Phanerota*, which have State  $B_2$ .

A single transformation series of these character states is indicated ( $A \rightarrow B_1 \rightarrow B_2$ ).

Although State  $B_1$  occurs in a few bolitocharines and some other aleocharines, these conditions are probably independently derived in these groups. In addition, the invariant occurrence of State  $B_1$  among all gyrophaenines except *Probrachida* (here State  $B_2$  is considered a secondary modification of State  $B_1$ ) indicates that State  $B_1$  probably evolved only once (perhaps twice, depending on relationships of *Brachida*; see Phylogenetic Analysis) within the gyrophaenines.

Therefore this character is useful for phylogenetic analysis.

Character 26 — Pronotum: sinuosity of the base. — States of this character among gyrophaenines are arranged in a continuously varying transformation series. However, this series is conveniently, although arbitrarily, divided into three character states: 1) hind margin of pronotum markedly bisinuate (*A*); 2) hind margin of pronotum slightly bisinuate (*B*<sub>1</sub>); and 3) hind margin of pronotum not bisinuate (*B*<sub>2</sub>). Based on both in-group and out-group comparisons, State *A* is considered plesiotypic. A markedly bisinuate hind margin of the pronotum (State *A*) is rather widely distributed in many groups of gyrophaenines. Reduction of bisinuations to a smoothly rounded hind margin appears to be most commonly associated with subsequent narrowing of the pronotum, an apotypic character state (see Character 28). In addition, State *A* is widely distributed within the Aleocharinae. Bolitocharines, however, do not have a bisinuate hind margin of the pronotum. Under this interpretation, State *B*<sub>2</sub> in bolitocharines is derived independently from State *B*<sub>2</sub> in gyrophaenines. A single transformation series is indicated (*A*→*B*<sub>1</sub>→*B*<sub>2</sub>). Because the states are arbitrary divisions of a continuum, and because of the probably multiple derivation of apotypic states within gyrophaenines, this character has very limited use for phylogenetic inference.

Character 27 — Pronotum: median emargination of base. — Two states are recognized: 1) hind margin of pronotum without a medial emargination (*A*), and 2) hind margin of pronotum with a broad to more or less acute medial emargination (*B*). State *A* is considered plesiotypic. It is the condition among most gyrophaenines, all bolitocharines, and most other aleocharines.

State *B* is uncommon among gyrophaenines and distributed in groups which are phylogenetically widely separated. It has probably been derived a number of times independently. Therefore, this character is not very useful for phylogenetic analysis.

Character 28 — Pronotum: shape. — Three states are recognized: 1) pronotum more or less markedly transverse (*A*); 2) pronotum more or less broadly oval (*B*<sub>1</sub>); and 3) pronotum more or less subquadrate (*B*<sub>2</sub>). Of these, State *A* is considered plesiotypic, based primarily on in-group comparisons. State *A* characterizes members of a number of genera of aleocharines. However, all bolitocharines that I have examined have States *B*<sub>1</sub> and *B*<sub>2</sub>. Occurrence of State *A* among a number of different groups of gyrophaenines, usually in association with states of other pronotal characters believed to be plesiotypic, suggests that this state is plesiotypic within the Gyrophaenina.

Because of the probable multiple origin of apotypic states among gyrophaenines, this character has limited use for phylogenetic inference.

Character 29 — Pronotum: flexion of lateral border. — Degree of ventral flexion of lateral borders of the pronotum among gyrophaenines is arranged in a continuum, from extremely deflexed to not deflexed. This continuum is conveniently, though arbitrarily, divided into three states: 1) lateral borders of pronotum moderately to slightly deflexed (*A*); 2) lateral borders of pronotum not at all or very slightly deflexed (*B*); and 3) lateral borders of pronotum very markedly deflexed (*C*). Of these State *A* is considered plesiotypic based on both in-group and out-group comparisons. Many aleocharines have a moderately convex pronotum. This prompted Seevers (1978) to suggest that the generalized condition of the aleocharine pronotum was rather convex, and flattening of the pronotum is derived. However, most bolitocharines have State *B* of this character. State *A* is widely distributed among gyrophaenines and occurs in at least some members of almost all genera. State *B* appears to have been derived several times independently: however, among gyrophaenines, very markedly flattened pronota only occur among species of *Gyrophaena* and *Phanerota*.

Very markedly convex pronotum (State C) is also considered derived (modified from State A). This condition is limited among gyrophaenines to members of *Brachychara*, *Adelarthra* and *Encephalus*.

Therefore, two transformation series are suggested in this character ( $A \rightarrow B$  and  $A \rightarrow C$ ).

Ambiguity of assigning conditions observed in specimens, and probable multiple origin of derived states among gyrophaenines make this character of very limited value for phylogenetic inference.

Character 30 — Hypomera: visibility. — Expression of this character is correlated with expression of Character 29, as discussed above under Structural Features. As in Character 29, the states are arranged in a continuum, arbitrarily divided into three states: 1) hypomera not visible in lateral view ( $A$ ); 2) hypomera narrowly visible in lateral view ( $B_1$ ); and 3) hypomera broadly or in large part visible in lateral view ( $B_2$ ). State  $A$  is considered plesiotypic. Justification for this hypothesis is very similar to that presented for polarity of Character 29. Invisibility of the hypomera in lateral view is probably plesiotypic for aleocharines as a group (Seevers, 1978), and State  $A$  is widely distributed among aleocharines and gyrophaenines. However, as far as is known, all bolitocharines have States  $B_1$  or  $B_2$  of this system. Under the hypothesis presented above, apotypic states among bolitocharines are derived independently of similar apotypic states in gyrophaenines. Among gyrophaenines, apotypic states, and particularly State  $B_2$ , are widely distributed only in the genera *Gyrophaena*, *Phanerota* and a few species of *Eumicrota*. However, usefulness of this character for phylogenetic inference is somewhat limited by the presence of all three character states ( $A$ ,  $B_1$ ,  $B_2$ ) within *Gyrophaena*. Some examples of State  $A$  within *Gyrophaena* may be secondary derivation of this condition from a more apotypic state. However, among some groups (e.g., *Gyrophaena hubbardi* Seevers and related species) State  $A$  of this character is associated with other presumed plesiotypic states of pronotal characters.

Character 31 — Scutellum: visibility. — Two states are recognized: 1) scutellum visible in dorsal view ( $A$ ), and 2) scutellum hidden by the base of the pronotum in dorsal view ( $B$ ). Based on in-group and out-group comparisons, State  $A$  is considered plesiotypic for gyrophaenines. Most aleocharines, all bolitocharines I have examined, and most gyrophaenines have State  $A$ .

The limited distribution of apotypic states makes it of relatively little use in phylogenetic inference at the genus level.

Character 32 — Elytron: latero-apical angle. — States of this character are arbitrary and rather ambiguous, but convenient, divisions of a continuous transformation series. These states are: 1) latero-apical angle of elytron markedly or deeply sinuate ( $A$ ); 2) latero-apical angle of elytron slightly or shallowly sinuate ( $B_1$ ); and 3) latero-apical angle of elytron not sinuate ( $B_2$ ). State  $A$  is considered plesiotypic, based primarily on out-group comparison. A great many aleocharines in a diversity of groups and all bolitocharines have State  $A$ . Hammond (1975) treated sinuate latero-apical angle of elytra as a uniquely derived character within the aleocharines in relation to the sister group (within which he included the Phloeocharinae, Tachyporinae, Trichophylinae and Habrocerinae). If Hammond is correct, then sinuate latero-apical elytral angles are plesiotypic for the Gyrophaenina. This is the interpretation accepted in this study.

If this hypothesis is correct, then a single transformation series is indicated based on progressive loss of sinuation of the latero-apical angles ( $A \rightarrow B_1 \rightarrow B_2$ ).

Because the apotypic states are regressive, they probably have been derived a number of times independently within Gyrophaenina. This character, therefore, is not very reliable for

phylogenetic inference within the gyrophaenines.

Character 33 — Prosternum: shape. — Two more or less ambiguous states are recognized: 1) prosternum markedly transverse (*A*), and 2) prosternum slightly to moderately transverse (*B*). State *A* is considered plesiotypic. This polarity is justified primarily by in-group comparisons, and is based mainly on correlation between the states of this character and those of Character 28. As discussed above, a transverse prosternum characterizes most specimens with markedly transverse pronota. If the hypothesis that the latter state is plesiotypic in gyrophaenines is accepted, then it follows that a markedly transverse prosternum, which is correlated with this condition, is also plesiotypic.

While this justification of this character polarity *A*→*B* is very weak, it is difficult to defend alternative hypotheses at this time. The alternative hypothesis that State *B* is plesiotypic is given some support by presence of this state in many bolitocharines. However, as noted in the discussion of Character 28, bolitocharines also have slightly transverse to subquadrate pronota, a presumed apotypic condition.

Because of the weak justification for polarity of this character, it has very limited use in phylogenetic inference.

Character 34 — Prosternum: medial ornamentation. — Four states are recognized: 1) prosternum with a tooth, carina, or knob medially (*A*); 2) prosternum with tooth, carina or knob reduced or absent (*B*); 3) prosternum with a transverse carina (*C*<sub>1</sub>); and 4) prosternum without a transverse carina (*C*<sub>2</sub>). State *A* is considered plesiotypic, justified primarily on the basis of out-group comparisons. This state is widespread among aleocharines and characterizes all bolitocharines. Among gyrophaenines, apotypic states are limited to members of the "*Gyrophaena*" lineage and *Probrachida* and *Brachida*, and is probably derived independently in each of these lineages. State *B* is not known among gyrophaenines, but is an inferred condition which seems to be required if the above hypothesis is correct. (It is possible, however, that the condition in members of the "*Brachida*" lineage represents State *B* instead of State *C*<sub>2</sub>. If so, it is indistinguishable from State *C*<sub>2</sub> found in some species of *Gyrophaena* and *Phanerota*.) State *C* does not seem directly derivable from State *A* without previous reduction of the medial ornamentation.

If the above hypothesis is correct, a single transformation series is indicated in which the medial ornamentation of the prosternum is reduced or lost, followed subsequently by development of a transverse carina on the prosternum. Finally, transverse carina is lost in some species (*A*→*B*→*C*<sub>1</sub>→*C*<sub>2</sub>).

This character has limited use for phylogenetic inference, and must be used with caution because two independently derived conditions (*B* and *C*<sub>2</sub>) may be indistinguishable, and also because some apotypic states are regressive.

Character 35 — Mesosternum: development of carina. — Four states are recognized: 1) mesosternum with a well developed median longitudinal carina from anterior margin to apex of mesosternal process (*A*); 2) median longitudinal carina more or less reduced, not complete to end of mesosternal process (*B*); 3) median longitudinal carina modified to a low, diffuse, broad ridge (*C*); and 4) median longitudinal carina absent (*D*). Based on both in-group and out-group comparisons, State *A* is considered plesiotypic. The presence of a median longitudinal carina on the mesosternum is widespread among the aleocharines. It is present in all bolitocharines that I have examined, though in this group there has been secondary modification to State *B* in many species. These facts, in addition to the presence of State *A* in a number of genera of gyrophaenines, provide strong support for the hypothesis that State *A* was the condition found

in the ancestor of the gyrophaenines.

Because all apotypic states are regressive, a number of different, morphologically indistinguishable transformation series are possible based on the above states. These are: 1) reduction of the posterior carina ( $A \rightarrow B$ ); 2) modification of the carina to a low, diffuse ridge (may be derived from either State  $A$  or  $B$ ) ( $A \rightarrow C$ ;  $B \rightarrow C$ ); and 3) complete loss of the median longitudinal carina, derived from any other state ( $A \rightarrow D$ ;  $B \rightarrow D$ ;  $C \rightarrow D$ ).

Because apotypic states are regressive, this character must be used with caution in phylogenetic inference within the gyrophaenines.

Character 36 — Intercoxal processes: relative length. — Two states are recognized: 1) mesosternal process extended to middle or slightly posterior to middle of middle coxae ( $A$ ), and 2) mesosternal process extended to or almost extended to posterior margin of mesocoxal cavities ( $B$ ). These character states are rather ambiguous, and intermediates between these states make this character rather difficult to use.

State  $A$  is probably most similar to the plesiotypic condition for gyrophaenines, based primarily on out-group comparisons. State  $A$  is the condition in most bolitocharines, and is widely scattered among gyrophaenines. However, variation in this system is inadequately understood. Intermediate conditions between these two states make interpretation difficult. It seems likely that apotypic states have been derived a number of times independently. Therefore, this character should be used with caution for phylogenetic inference.

Character 37 — Intercoxal processes: separation. — Two states are recognized: 1) mesosternal and metasternal processes more or less separated, isthmus present ( $A$ ), and 2) mesosternal and metasternal processes more or less contiguous, isthmus absent ( $B$ ). Based primarily on out-group comparisons, State  $A$  is considered plesiotypic. It is the condition of most bolitocharines and many other aleocharines. State  $B$  characterizes all gyrophaenines except specimens of *Agaricochara* which have a very short isthmus. Contiguous intercoxal processes are so invariable within Gyrophaenina that it suggests that slightly separated intercoxal processes in *Agaricochara* species may be secondary.

State  $B$  in specimens of a few species of bolitocharines, and some other aleocharines, is almost certainly exemplary of independent evolution of this condition in these groups.

Because of uniform distribution of the plesiotypic state of this character among gyrophaenines, this is not useful for phylogenetic inference within this subtribe. It does provide additional evidence that gyrophaenines are monophyletic. However, presence of State  $A$  in specimens of *Agaricochara* is anomalous within this hypothesis.

Character 38 — Intercoxal processes: condition of juncture. — Two states are recognized: 1) junction between mesosternal and metasternal process truncate or broadly rounded, with a distinct suture ( $A$ ), and 2) junction between intercoxal processes fused, suture invisible ( $B$ ). State  $A$  is considered plesiotypic, based on both in-group and out-group comparisons. Completely fused mesosternal and metasternal processes were not present among the bolitocharines I examined, and they are not common among other aleocharines. State  $A$  characterizes most gyrophaenines. From this condition, State  $B$  has apparently been derived independently a number of times (often within a single genus).

Because of the probable multiple origin of the apotypic condition, this character is of very limited use for phylogenetic inference.

Character 39 — Metepisternal setae. — Four states are recognized: 1) setae on metepisternum numerous, uniformly and irregularly distributed ( $A$ ); 2) setae on metepisternum in 2 irregular rows ( $B_1$ ); 3) setae on metepisternum in a single well

differentiated row ( $B_2$ ); and 4) setae on metepisternum absent or very few scattered setae restricted to posterior third or less ( $C$ ). Justification for considering State  $A$  plesiotypic is available from both in-group and out-group comparisons. This state characterizes most bolitocharines and many other aleocharines, but among gyrophaenines is represented only in specimens of some species of *Probrachida* and *Brachida*. These groups arise near the base of the cladogram and have a number of other plesiotypic character states.

States of this character are arranged in several transformation series. The first involves progressive loss of setae of the metepisternum by reduction of the number of rows of setae ( $A \rightarrow B_1 \rightarrow B_2$ ). The second series involves complete loss of the setae on the metepisternum. However, this condition could conceivably be derived from any of the other states ( $A \rightarrow C$ ;  $B_1 \rightarrow C$ ;  $B_2 \rightarrow C$ ). At present it is impossible to distinguish between the end results of these transformation series.

Since the apotypic states involve regression, the character must be used with caution. However, as a comparative character, it is very useful for analysis of some lineages.

Character 40 — Metepisternum: carina. — Two states are recognized: 1) setose area on metepisternum not delimited anteriorly and ventrally by a carina ( $A$ ), and 2) setose area on metepisternum delimited anteriorly and ventrally by a slight to moderately developed carina ( $B$ ). Based on both in-group and out-group comparison, State  $A$  is considered plesiotypic. It characterizes most bolitocharines, and is widely distributed among other aleocharines. Among gyrophaenines, State  $A$  characterizes members of most genera.

State  $B$  has been independently derived in a few bolitocharines and several other aleocharine lineages, suggesting that the apotypic state may also be of multiple origin within Gyrophaenina. The condition of the metepisternum of most species of the "*Probrachida*" lineage may be confusing. In these specimens, the setose area of the metepisternum is depressed so that the setae are in a well defined groove. However, the anterior and ventral edges of this groove do not appear to be homologous to the carina located in this position in other gyrophaenines.

A problem in using this character is interpretation of the condition. The carina may be very faint and present only anteriorly, or it may be quite distinct and form a complete anterior and ventral boundary for the setose area. Intermediates between the conditions also occur. I have considered all these carinate conditions equivalent under State  $B$ .

This character is useful for phylogenetic inference. However, because of the possibility of multiple origin of the derived conditions, it must be used with caution.

Character 41 — Abdomen: number of terga transversely impressed. — Three states are recognized: 1) terga 3-6 moderately transversely impressed ( $A$ ); 2) terga slightly impressed, one or more of 3-5 without impressions ( $B_1$ ); and 3) all terga without transverse impressions ( $B_2$ ). Of these, State  $A$  is considered plesiotypic. Justification for this hypothesis is from both in-group and out-group comparisons. State  $A$  is found in all bolitocharines and in most other aleocharines. In addition, State  $A$  is the condition in most gyrophaenines and is found in specimens of almost all lineages.

A single transformation series is indicated for the states based on progressive loss of transverse impressions on the abdominal terga ( $A \rightarrow B_1 \rightarrow B_2$ ).

Difficulty in interpreting the conditions of this character is possible. Because apotypic states are regressive, the probability of multiple origin of States  $B_1$  and  $B_2$  is very high. Therefore, this character has very limited value in phylogenetic inference within the gyrophaenines.

Character 42 — Tergum 10: shape of medial setose area. — Five states are recognized: 1) medial setose area of tergum 10 more or less quadrate with numerous setae ( $A$ ); 2) medial

setose area on tergum 10 more or less quadrate with fewer, more widely scattered setae (*B*); 3) medial setose area on tergum 10 chevron-shaped (inverted V-shaped, point directed anteriorly) with numerous setae not in distinct rows (*C*<sub>1</sub>); 4) medial setose area on tergum 10 chevron-shaped, setae few, in one or two (in some specimens, slightly a third) well developed rows (*C*<sub>2</sub>); and 5) medial setose area on tergum 10 V-shaped (point of "V" directed posteriorly), setae few, in one or two distinct rows (*D*). Based on both in-group and out-group comparisons, State *A* is hypothesized to be plesiotypic. It is widespread among aleocharines and is found among specimens of phylogenetically widely separated groups of gyrophaenines. In addition, State *A* is the condition from which all other conditions of this character could most easily be derived within gyrophaenines.

The alternate hypothesis, that State *C*<sub>1</sub> is plesiotypic, is given some support by the fact that this state characterizes bolitocharines. It is also the condition in many other groups of aleocharines, particularly some Oxypodini. However, it seems most parsimonious to conclude that the structurally less complex subquadrate setal patch is the true plesiotypic condition for the aleocharines as a whole. If so, then State *C*<sub>1</sub> has been independently evolved in bolitocharines, many groups of aleocharines, and some gyrophaenines.

If this hypothesis is correct, then at least three transformation series are indicated. The first is simple reduction in number and density of the setae (*A*→*B*). The second series involves loss of setae posteriorly and medially, giving an emarginate setose area, with the trend continued to produce a chevron-shaped setose area composed of well developed rows of setae (*A*→*C*<sub>1</sub>→*C*<sub>2</sub>). A third series involves loss of antero-medial and postero-lateral setae producing a V-shaped setose area (*A*→*D*). Presumably the second and third of these series could involve State *B* as an intermediate condition.

Although the apotypic states are regressive, the patterns of loss are not uniform in the different transformation series. Therefore, though it seems likely that States *C*<sub>1</sub> and *C*<sub>2</sub> have been independently derived several times in the gyrophaenines (see Morphological Adaptations), this character, when used with caution, is very useful for phylogenetic inference.

Character 43 — Tergum 10: structure of medial setae. — Three states are recognized: 1) setae on tergum 10 more or less long, setiform, unmodified (*A*); 2) setae on tergum 10 more or less short and stubby, setiform (*B*<sub>1</sub>); 3) setae on tergum 10 flattened, more or less subspatulate (*B*<sub>2</sub>). Justification for considering State *A* plesiotypic comes from in-group and out-group comparisons. This is the condition of bolitocharines and most other aleocharines. State *A* also occurs in phylogenetically diverse groups of gyrophaenines.

If the hypothesis about character state polarity is correct, either one or two transformation series are possible based on these character states. It seems most likely that State *B*<sub>1</sub> is derived from State *A*. However, State *B*<sub>2</sub> may be derived from either State *A* or *B*<sub>1</sub> (*A*→*B*<sub>2</sub>; *A*→*B*<sub>1</sub>→*B*<sub>2</sub>). It is not possible to distinguish between the end products of these two transformation series at this time.

Although multiple origin of apotypic states is possible within the gyrophaenines, the system is useful in phylogenetic inference within the group, especially when used in correlation with other characters.

Character 44 — Spermatheca: latero-apical plate. — Two states are recognized: 1) latero-apical plate absent (*A*), and 2) latero-apical plate present (*B*). State *A* is almost certainly plesiotypic, based on out-group comparison. Although the structure of the spermatheca of aleocharines has not been studied in detail, and spermathecal structure of many groups is unknown, a latero-apical plate is known only among members of the Gyrophaenina. In



addition, females of all gyrophaenines, except for a few species of *Probrachida*, have such a plate. Members of those few species of *Probrachida* which lack this plate are most parsimoniously considered to have lost this structure, since it occurs in females of closely related species. The latero-apical plate (State *B*), is, therefore, almost certainly a uniquely derived characteristic within the subtribe Gyrophaenina.

Since females of all gyrophaenines possess State *B* of this character, it is not useful for phylogenetic inference within this subtribe. However, this character is of great value in supporting the hypothesis that gyrophaenines are monophyletic.

Character 45 — Spermatheca: modifications. — Three states are recognized: 1) spermatheca simple, without elongate neck (*A*); 2) spermatheca with neck elongate distal to the latero-apical plate, neck often twisted or convoluted (*B*); 3) spermatheca with neck elongate proximal to the latero-apical plate, neck often twisted or convoluted (*C*). Based primarily on in-group comparisons, State *A* is considered plesiotypic. It characterizes females of a number of lineages of gyrophaenines. States *B* and *C* are limited to single lineages, and it is most parsimonious to consider them independently derived.

This character has limited use for phylogenetic inference within the gyrophaenines. It is most useful in supporting hypotheses about the monophyly of those groups within the subtribe which have the derived states.

Character 46 — Median lobe of the aedeagus. — For simplicity of representation, only two states are recognized. However, a large number of relatively plesiotypic and apotypic states can be recognized among gyrophaenine aedeagi. Outgroup comparison with bolitocharines and other aleocharine groups suggests that in the relatively plesiotypic condition, the median lobe of gyrophaenines has a simple, lobe-like apical process and a relatively short, unsclerotized, tube-like flagellum (State *A*). Relatively apotypic conditions of the median lobe include modification of the apical process to very slender, blade-like or highly complex structures, and modification of the flagellum to very slender, elongate, whip-like structures, or highly complex and more or less sclerotized structure (State *B*). Therefore, for this character, plesiotypic and apotypic conditions discussed in cladistic analysis are not specific conditions, but rather conditions relative to that hypothesized to have been present in the common ancestor of two lineages.

Because general form of the median lobe is relatively uniform within a group, this is a very useful character for phylogenetic analysis. This character can be treated as a number of more specific systems for use at other levels of analysis.

Character 47 — Parameres. — Justification for this character is similar to that of Character 46. Only two states are recognized. In-group and out-group comparisons with bolitocharines and other aleocharines suggest that in the plesiotypic condition, the apical lobe of the paramerite of gyrophaenine parameres is symmetrical, relatively simple, elongate, and with four more or less equal setae located near apex (State *A*). Relatively apotypic conditions of the parameres include modifications of the apical lobes to be asymmetrical, or very elongate, with setae very unequal in size and not all located near apex (State *B*). The specific condition considered apotypic is discussed in the appropriate section of the cladistic analysis.

Because relatively apotypic conditions are uniform in some groups, this is a useful character for phylogenetic analysis. This character can also be resolved to a number of more specific characters useful at other levels of analysis.

Table 1. Plesiotypic and Apotypic States of Characters Discussed in Text (letters in parentheses are character state designations used in text).

<i>Character</i>		<i>Plesiotypic</i>	<i>Apotypic</i>
1	<b>Body setae:</b> microsetae	-numerous, more or less short, densely and uniformly distributed over body (A)	-more or less long and silky, densely and uniformly distributed (B) -short, number reduced, body subglabrous (C <sub>1</sub> ) -short, number very reduced, body more or less glabrous (C <sub>2</sub> )
2	<b>Body setae:</b> macrosetae	-small, difficult to distinguish from microsetae A	-larger, easily distinguished from microsetae (B <sub>1</sub> )
3	<b>Sculpture</b>	-uniformly reticulate (A)	-extremely large, very conspicuous (B <sub>2</sub> ) -obsolete or smooth on one or more body parts (B <sub>1</sub> )
4	<b>Head:</b> medial macrosetae	-pair of macrosetae present medially on vertex (A)	-absent, body integument uniformly smooth (B <sub>2</sub> ) -macrosetae absent on vertex (B)
5	<b>Head:</b> infraorbital carina	-well developed, complete ventrally (A)	-incomplete, reduced or absent ventrally (B)
6	<b>Head:</b> lateral macrosetae	-lateral macrosetae absent (A)	-2 lateral macrosetae on each side of dorsal surface of head (B)
7	<b>Eyes:</b>	-size moderate (A)	-extremely large, prominent (B)
8	<b>Antenna:</b> article 4	-similar in setation and general shape to articles 5-10 (A)	-similar in setation and general shape to articles 1-3 (B)
9	<b>Labrum:</b> number of setae	-numerous setae in addition to basic setal pattern (A)	-few or no setae in addition to basic setal pattern (B)

(continued on next page)

Table 1 (continued)

Character	Plesiotypic	Apotypic
10 <b>Labrum:</b> $\alpha$ -sensillum	-filiform, seta-like (A)	-thickened, hyaline (B)
11 <b>Labrum:</b> $\epsilon$ -sensillum	-large indistinguishable from labral setae (A)	-setose but much smaller than labral setae (B <sub>1</sub> )
12 <b>Labrum:</b> lateral sensilla row (position)	-sensilla near or at lateral margin of labrum (A)	-reduced, small, peg-like (B <sub>2</sub> ) -sensilla more or less distant from lateral margin of labrum (B)
13 <b>Labrum:</b> lateral sensilla row (development)	-4 or 5 well developed sensilla (A)	-number and development of sensilla reduced (B)
14 <b>Labrum:</b> A.L. 1 and A.L. 2	-origin more or less distant from margin of labrum (A)	-origin at margin of labrum (B)
15 <b>Labrum:</b> internal setose areas	-densely setose area present internally on each side of labrum (A)	-densely setose area absent internally on each side of labrum (B)
16 <b>Mandibles:</b> form of apex	-not bifid at apex (A)	-left mandible bifid at apex (B)
17 <b>Mandibles:</b> internal tooth	-right mandible with well developed internal tooth (A)	-both mandibles without well developed internal tooth (B)
18 <b>Lacinia:</b> form of apex	-more or less acute (A)	-both mandibles with well developed internal tooth (C)
19 <b>Lacinia:</b> apical teeth	-relatively few, in a loosely defined patch, slightly, or not at all differentiated from lateral spines or teeth (A)	-obliquely truncate (B) -numerous, closely spaced, in well defined patch, well differentiated from lateral spines or teeth (B)

(continued on next page)

Table 1 (continued)

<i>Character</i>		<i>Plesiotypic</i>	<i>Apotypic</i>
20	<b>Lacinia:</b> inner face (teeth)	-numerous, densely arranged, often spine-like teeth present (A)	-few, more or less scattered teeth present (B <sub>1</sub> ) -teeth absent (B <sub>2</sub> )
21	<b>Lacinia:</b> inner face (setae)	-very numerous, densely arranged, irregularly scattered (A)	-less numerous, few to many, more or less loosely and irregularly scattered (B <sub>1</sub> ) -few to many in a well differentiated vertical row (B <sub>2</sub> )
22	<b>Galea:</b> apical setae (arrangement)	-numerous, in close numerous rows (8-10 or more ) (A)	-numerous, rows fewer, (5-8), but not close (B <sub>1</sub> ) -less numerous, in 4 well separated rows (B <sub>2</sub> )
23	<b>Galea:</b> apical setae (str.)	-long, filiform, setose (A)	-flattened, subspatulate or plate-like (B)
24	<b>Labium:</b> form of ligula	-elongate, bifid at apex (inferred) (A)	-short, entire, protruded and parallel sided (B) -short, entire, broadly rounded (C) -short, protruding, parallel sided, divided 1/2 to 1/3 distance to base (D <sub>1</sub> ) -short, protruding, parallel sided, divided almost or fully to base (D <sub>2</sub> )
25	<b>Labium:</b> no. med. setae	-2 medial setae (A)	-elongate, parallel sided, divided in anterior 1/3 (E) -1 medial seta (B <sub>1</sub> ) -medial setae absent (B <sub>2</sub> )
26	<b>Pronotum:</b> hind margin (sinuosity)	-markedly bisinuate (A)	-slightly bisinuate (B <sub>1</sub> ) -not bisinuate (B <sub>2</sub> )

(continued on next page)

Table 1 (continued)

Character	Plesiotypic	Apotypic
27 <b>Pronotum:</b> hind margin (emargination)	–without medial emargination (A)	–with medial emargination (B)
28 <b>Pronotum:</b> shape	–markedly transverse (A)	–broadly oval (B <sub>1</sub> )
29 <b>Pronotum:</b> lateral borders	–moderately to slightly deflexed (A)	–more or less subquadrate (B <sub>2</sub> )
30 <b>Hypomeron:</b> visibility	–not visible in lateral view (A)	–not at all or very slightly deflexed (B)
31 <b>Scutellum:</b> visibility	–visible in dorsal view (A)	–very markedly deflexed (C)
32 <b>Elytron:</b> latero-apical angle	–markedly or deeply sinuate (A)	–narrowly visible in lateral view (B <sub>1</sub> )
33 <b>Prosternum:</b> shape	–markedly transverse (A)	–broadly or in large part visible in lateral view (B <sub>2</sub> )
34 <b>Prosternum:</b> medial ornamentation	–tooth, carina or knob medially (A)	–hidden in dorsal view (B)
35 <b>Mesosternum:</b> carina (development)	–well developed medial carina from anterior margin to apex of metasternal process (A)	–slightly or shallowly sinuate (B <sub>1</sub> )
		–rectilinear, not at all sinuate (B <sub>2</sub> )
		–slightly to moderately transverse (B)
		–tooth, carina or knob absent (B)
		–transverse carina (C <sub>1</sub> )
		–transverse carina absent (C <sub>2</sub> )
		–medial carina more or less reduced, not complete to end of mesosternal process (B)
		–medial carina modified to low, diffuse, broad ridge (C)
		–carina absent (D)

(continued on next page)

Table 1 (continued)

Character	<i>Plesiotypic</i>	<i>Apotypic</i>
36 <b>Intercoxal processes:</b> relative lengths	-mesosternal process extended to middle or slightly beyond middle of mesocoxal cavities (A)	-mesosternal process attaining or almost attaining posterior margin of mesocoxal cavities (B)
37 <b>Intercoxal processes:</b> separation	-processes more or less separate, isthmus present (A)	-processes contiguous, isthmus absent (B)
38 <b>Intercoxal processes:</b> juncture	-truncate or broadly rounded, with a distinct suture (A)	-fused, suture invisible (B)
39 <b>Metepisternal setae</b>	-numerous, uniformly and irregularly distributed (A)	-numerous, in 2 irregular rows (B <sub>1</sub> ) -in a single well differentiated row (B <sub>2</sub> ) -setae absent or very few, restricted to posterior 1/3 or less (C)
40 <b>Metepisternum:</b> carina	-setose area not delimited anteriorly and ventrally by a carina (A)	-setose area delimited anteriorly and ventrally by a slightly to moderately developed carina (B)
41 <b>Abdomen:</b> number of transversely impressed tergites	-3-6 moderately markedly transversely impressed (A)	-slightly impressed, one or more of 3-5 without impressions (B <sub>1</sub> ) -all tergites without transverse impressions (B <sub>2</sub> )

(continued on next page)

Table 1 (continued)

	Character	<i>Plesiotypic</i>	<i>Apotypic</i>
42	<b>Tergum 10:</b> medial setose area	—more or less quadrate, with numerous setae (A)	—more or less quadrate, with fewer, more widely scattered setae (B) —chevron-shaped, with numerous setae not in distinct rows (C <sub>1</sub> ) —chevron-shaped, with setae in 1 or 2 well developed rows (C <sub>2</sub> ) —V-shaped, few setae in 1 or 2 well developed rows (D) —more or less short and stubby, setiform (B <sub>1</sub> ) —flattened, more or less subspatulate (B <sub>2</sub> ) —latero-apical plate present (B) —neck elongate distal to latero-apical plate (B) —neck elongate proximal to latero-apical plate (C) —apical process elongate, very slender, blade-like, asymmetrical or highly complex; flagellum very slender, elongate, whip-like or complex and more or less sclerotized (B)
43	<b>Tergum 10:</b> medial setae (structure)	—more or less long, setiform, unmodified (A)	
44	<b>Spermatheca:</b> latero-apical plate	—latero-apical plate absent (A)	
45	<b>Spermatheca:</b> modification	—simple, without elongate neck (A)	
46	<b>Aedeagus:</b> median lobe	—apical process simple, lobe-like; flagellum short, unscerotized, tube-like (A)	
47	<b>Aedeagus:</b> parameres	—apical lobe of paramerites symmetrical, simple, elongate, with 4 more or less equal setae near apex (A)	—apical lobe of paramerites asymmetrical or very elongate, with setae very unequal and not all near apex (B)

TABLE 2  
Distribution of plesiotypic and apotypic character states among gyrophaenine genera

Character	Bolitocharina subt	Probrachida	Brachida	Agaricochara	Agaricomorpha	Brachychara	Adelathra	Sternotropa	Pseudolligota	Neobrachida	Gyrophaena	Phaneroa	Eumicrota	Encephalus
1 Body setae: microsetae	A, C <sub>1</sub>	B	B <sub>1</sub> , C <sub>1</sub>	A	A	C <sub>1</sub>	C <sub>2</sub>	A, C <sub>1</sub>	A, C <sub>1</sub>	C <sub>1</sub>	A, C <sub>1</sub> , C <sub>2</sub> , C <sub>3</sub>	C <sub>1</sub> , C <sub>2</sub>	A	C <sub>2</sub>
2 Body setae: macrosetae	A	A, B <sub>1</sub>	A, B <sub>1</sub>	A	A	A, B <sub>1</sub>	B <sub>1</sub>	A, B <sub>1</sub>	A	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	A, B <sub>1</sub>	A, B <sub>1</sub>
3 Sculpture	A	A, B <sub>1</sub>	A	A	A, B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	A, B <sub>1</sub> , B <sub>2</sub>	A, B <sub>2</sub>	B <sub>2</sub>	A, B <sub>1</sub> , B <sub>2</sub> , A, B <sub>3</sub> , B <sub>4</sub>	A, B <sub>1</sub> , B <sub>2</sub>	A	A
4 Head: medial macrosetae	B	B	A	B	B	(a)	B	B	B	B	B, A	B	B, A	B
5 Head: infraorbital carina	A	A	A	A	A	A	A	A, B	B	A	A	A	A	A
6 Head: lateral macrosetae	A	A	A	A	A	A	A	A	A	A	A	A, B	A	A
7 Eyes	A	A	A	A	A	A	A	A	A	A	A	B	A	A
8 Antenna: article 4	A, B	A	A, B	B	B	B	B	B	B	B	A	B	A	A
9 Labrum: number of setae	A	A, B	A, B	B	B	B	B	B	B	?	B	B	B	B
10 Labrum: α sensillum	A, B	A, B	B	A	A	A	A	A	A, B	?	A	A	A	B
11 Labrum: ε sensillum	B <sub>1</sub>	A, B <sub>1</sub> , B <sub>2</sub> , A, B <sub>3</sub> , B <sub>4</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	?	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>
12 Labrum: lateral sensilla (position)	A, B	A	A	B	B	A	A	A	—	?	B	B	B	B
13 Labrum: lateral sensilla (dvp/mnt)	A, B	A	A, B	A	A	A	B	B, A	B	?	A, B	A	A	B
14 Labrum: AL 1 and AL 2	A	A	A	B	B	B	B	B	B	?	B	B	B	A
15 Labrum: internal setose areas	?	A	A, B	B	B	B	B	B	B	?	B	B	B	B
16 Mandibles: form of apex	A	A, B, C	B	A	A	A	A	A	A	A	A	A	A	A
17 Mandibles: internal tooth	A	A, B	A	A	A	A	A	A	A, B	?	A	A	A	A
18 Lacinia: form of apex	A	B	B	B	B	B	B	B	B	B	B	B	B	B
19 Lacinia: apical teeth	A	B	B	B	B	B	B	B	B	B	B	B	B	B
20 Lacinia: inner face (teeth)	A	B <sub>1</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>
21 Lacinia: inner face (setae)	A	A, B <sub>1</sub>	A, B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>2</sub>	?	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>
22 Galea: apical setae (larrngmnt)	A	A, B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	?	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>
23 Galea: apical setae (struct.)	A	A	A, B	B	B	B	B	B	B	B	B	B	B	B
24 Labium: form of ligula	A	C	C	D <sub>1</sub>	D <sub>1</sub>	D <sub>1</sub>	D <sub>1</sub>	D <sub>1</sub>	D <sub>1</sub>	E	B	B	B	C

cont. next page



TABLE 2 continued

Character	subtribe Bolitocharina	Probrachida	Brachida	Agaricocharena	Agaricomorpha	Brachychara	Adelarthra	Sternotropa	Pseudoligota	Neobrachida	Gyrophaena	Phanerocha	Eumicrota	Encephalus
25 Labium: number of medial setae	A, B	A	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>
26 Pronotum: hind margin (sinuosity)	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>1</sub>	A, B <sub>1</sub>	A	A	A	B <sub>1</sub>	B <sub>1</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>2</sub>	A, B <sub>1</sub>	B <sub>2</sub>
27 Pronotum: hind margin (emarg.)	A	B	A	A	A	A	A	A	A	A	A, B	A	A	B
28 Pronotum: shape	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	A	A	A	A	A	A	A, B	B <sub>1</sub>	A, B	A
29 Pronotum: lateral borders	B	A	A	B	A	C	C	A	A	A	A, B	B	A, B	C
30 Hypomeron: visibility	B	A	A	B	A	A	A	A	A	A	A, B	B	A, B	A
31 Scutellum: visibility	A	A	A	A	A	A	A	A	A	A	A, B	B	A, B	A
32 Elytron: latero-apical angle	A	B <sub>2</sub>	B <sub>2</sub>	B <sub>1</sub>	A	B	B	A, B	B	A	A	A	A	A
33 Prosternum: shape	A, B	B	B	A, B	A	A	A	A	A, B <sub>1</sub>	A	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	A, B <sub>1</sub>	B <sub>2</sub>
34 Prosternum: medial ornamentation	A	C <sub>2</sub>	C <sub>2</sub>	C <sub>1</sub>	A	A	A	A	A	A	B	B	A	A
35 Mesosternum: carina (dvlpmnt)	A, B	A, D	C, D	B	A, B	C	A	A, B	D	C	B, C <sub>1</sub> , C <sub>2</sub> , C <sub>3</sub>	D	B	C <sub>1</sub>
36 Intercostal processes: rel. lengths	A	B	B	A	A	A	?	A	?	A	A, B	A	A	B
37 Intercostal processes: separation	A, B	B	B	A	B	B	B	B	B	B	B	B	B	B
38 Intercostal processes: juncture	—, A	A	A	—	A, B	B	B	A, B	B	B	A, B	A	A, B	A
39 Metepisternal setae	A, B	A	A, B <sub>1</sub> , B <sub>2</sub>	B <sub>2</sub>	B <sub>1</sub> , B <sub>2</sub>	B <sub>1</sub>	C	B <sub>1</sub>	B, C	B	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	C
40 Metepisternum: carina	A, B	A	A	B	A, B	B <sub>1</sub>	A	A	A	A	A, B	A, B	A	A, B
41 Abdomen: # trnsv impress. terga	A	A	A	A	A, B <sub>1</sub>	B <sub>1</sub>	A	A	A	A	A, B	A	A	A, B
42 Tergum 10: medial setose area	C	A	A	A	C <sub>1</sub>	C <sub>2</sub>	B	C <sub>1</sub> , C <sub>2</sub>	B	C <sub>2</sub>	A, B	A, B	D	A, B
43 Tergum 10: medial setae (form)	A	A	A	B <sub>1</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>1</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>2</sub>	B <sub>2</sub>	7B <sub>1</sub>
44 Spermatheca: latero-apical plate	A	B	B	B	B	B	B	B	B	B	B	B	B	B
45 Spermatheca: modification	—	C	B	A	A	A	?	A	A	A	A, C	C	A	A
46 Aedeagus: median lobe	A	B	B	B	B	B	B	B	B	?	A, B	B	B	A
47 Aedeagus: parameres	A	A	A	A, B	A	A	B	B	B	?	A, B	A	A, B	A

### Phylogenetic Analysis

*Theoretical Considerations.*— I agree with Whitehead (1972) and Hammond (1975) that it is important to clearly present the theoretical, philosophical and methodological basis for an analysis. Without such a clear exposition of approach, subsequent critical evaluation is difficult or ineffective. In this section, I will present a brief review of the fundamental assumptions on which the following analysis is based.

The procedure used in this treatment for reconstructing the phylogenetic relationships of groups of gyrophaenines was originally developed by Hennig (1965, 1966). Since these first expositions on phylogenetic systematics (which will be referred to here as "cladistic analysis" or "cladism") the literature on cladistic methods, philosophy, and theoretical implications has become extensive. In addition, as Bonde (1977) and Gaffney (1979) have pointed out, the ideas and methods currently considered as parts of cladistic analysis are very diverse.

Major papers which have developed cladistic methods or theory, in addition to primary papers by Hennig (1965, 1966), include Brundin (1966, 1972), Cracraft (1974), Griffiths (1974), Hecht and Edwards (1977), Nelson (1972, 1973), Platnick (1977), Schaeffer, Hecht and Eldredge (1972), and Wiley (1975). Important papers concerned with philosophical aspects of systematics include Cracraft (1978), Hull (1970, 1974, 1979), Platnick (1979), and Platnick and Gaffney (1977, 1978). Major criticisms of cladistic methods have come from Ashlock (1974), Bock (1968), Darlington (1970), Mayr (1974) and Simpson (1975).

Three recent books (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981), while different in intent and approach, provide insight into contemporary concepts of phylogenetic inference.

I agree with Eldredge and Cracraft (1980) that reconstruction of the phylogenetic history of a group should be done using a method which is hypothetico-deductive in structure. That is, hypotheses about phylogenetic history must be presented in such a way that they can be critically evaluated, and, if inconsistent with additional evidence, be rejected. I believe that cladistic analysis is the presently available method most consistent with this requirement.

I accept the following methodological principles in relation to cladistic analysis: 1) monophyletic groups can be recognized only on the basis of uniquely shared, derived character states (autapotypy); 2) the sequence of cladistic events can be reconstructed by arranging monophyletic terminal taxa into progressively more comprehensive monophyletic groups based on shared characters which are uniquely derived at the given level of analysis; 3) the sequence of cladogenetic events in a lineage is best expressed by a dichotomous branching diagram or cladogram, though this may not be the most exact representation of the evolutionary history of the group.

It has been clear to most taxonomists for some time that grouping of organisms based on shared homologous structures is most useful. The major contribution of Hennig (1966) was recognition that there were two levels of homology. There are those homologous structures which are uniquely shared by all members of a taxon, and assumed to have been first derived in the most recent common ancestor of that taxon (apotypies); and there are homologous structures which are shared among members of a more inclusive taxon (plesiomorphies). De Jong (1980) pointed out that most authors who have used these terms have not been very precise and have often used them as synonyms. In this treatment, I have accepted De Jong's use of the terms synapotypy and autapotypy. Synapotypy is used to denote common possession of a derived condition whether it is of monophyletic or polyphyletic origin. Autapotypy is restricted to common possession of a derived character state of monophyletic origin.

Dichotomous cleavage of lineages is accepted here as a methodological principle. For species-level taxa, this is certainly an over-simplification, and is unlikely to accurately represent evolutionary events. However, a cladogram (*sensu* Hennig, 1966) is only intended to represent recency of common ancestry as indicated by distribution of shared derived characteristics. Accurate representation of evolutionary patterns such as ancestry and descent or more complex cleavages of ancestral species are matters for subsequent analysis (Eldredge and Cracraft, 1980).

Higher level taxa do not evolve by cleavage of ancestral species in the same sense that species do. If higher level taxa are required to be monophyletic in a strict sense (*sensu* Hennig, 1966) rather than in the sense of Simpson (1953), a dichotomous branching diagram should in principle accurately reflect both nearest common ancestor and branching sequence. In practice, though, this sequence may be very difficult to resolve. This is not true, however, if higher taxa are considered monophyletic in the sense of Simpson (1953) or if they are allowed to be paraphyletic. In the first instance (strict monophyly) ancestor-descendent relationships between higher taxa are meaningless since this would require that some of these taxa be paraphyletic, a situation not allowed by definition. In the second instance (monophyly *sensu* Simpson), ancestor-descendent relationships between higher taxa are meaningful.

This distinction is important since this revision is a treatment of higher level taxa. I have here accepted a strict definition of monophyly for higher level taxa.

*Cladistic Relationships.*— For convenience of discussion I designate informal names for the three major lineages of gyrophaenines: the “*Brachida*” lineage, the “*Sternotropa*” lineage, and the “*Gyrophaena*” lineage. The “*Brachida*” lineage includes two genera: *Probrachida* n. gen., and *Brachida*; the “*Sternotropa*” lineage, seven genera: *Sternotropa*, *Pseudoligota*, *Adelarthra*, *Agaricomorpha* n. gen., *Brachychara*, *Neobrachida*, and tentatively *Agaricochara*; and the “*Gyrophaena*” lineage, three genera: *Gyrophaena*, *Phanerota* and *Eumicrota*. For reasons given below, *Encephalus* is of uncertain placement and therefore not included in these informal groups.

Relationships of several genera are uncertain. The genera *Brachida*, *Adelarthra* and *Agaricochara* can be placed in several positions within the cladogram, depending on assumptions made about number and types of parallel evolution of character states within related lineages. Therefore, a series of alternative hypotheses about cladistic relationships of each of these genera is provided; each hypothesis is discussed and evaluated, and, where possible, the most parsimonious, based on available data, is chosen.

Relationships of two genera, *Neobrachida* and *Encephalus* are so unclear that they cannot be placed on the cladogram with confidence. Possibilities are discussed and problems in placing them phylogenetically are outlined. However, *Neobrachida* and *Encephalus* are not included in the cladogram in Figure 260.

Detailed discussion of the relationships of gyrophaenines within the Aleocharinae is seriously compromised by incomplete and inadequate knowledge of structural, behavioral and ecological diversity of this subfamily. Within the context of the present study, little can be done to remedy this situation. Detailed surveys of structural characters, particularly of mouthparts, of representatives of most major tribes and subtribes of aleocharines were undertaken. However, the large number of valid higher taxa of aleocharines and great structural diversity among them requires that such a survey must be quite superficial.

Several recent studies of groups within the Aleocharinae have provided additional background information about structural diversity, and I have relied rather heavily on these.

These include Hammond (1975), Sawada (1970, 1972), Klimaszewski (1979), and Seevers (1978).

The subtribe Gyrophaenina is placed in the tribe Bolitocharini by most authors. (A historical survey of classification of the gyrophaenines is given above). Traditionally, the tribe Bolitocharini has been comprised of those aleocharines with a 4-4-5 tarsal formula. As such, the tribe was very heterogenous and probably polyphyletic. Seevers (1978) removed several groups of aleocharines with specialized habits from the Bolitocharini and placed these in separate tribes.

While recognizing that the tribe Bolitocharini will almost certainly require additions or deletions as the aleocharines become better known, I regard Seevers' (1978) as the best available working concept of the tribe. Therefore, future reference to the tribe Bolitocharini will be the Bolitocharini *sensu* Seevers (1978). Among the aleocharines which Seevers retained in the Bolitocharini, he recognized six "groups", which appear equivalent to the subtribe category as used in this study. Members of the Bolitocharini are all either inhabitants of fresh mushrooms, or subcortical. Although the group still remains rather heterogenous, gyrophaenines share a number of characteristics with other members of the tribe. These include: 1) the 4-4-5 tarsal formula; 2) small rows of minute denticles or teeth on the molar region of the mandibles; and 3) similarities in the median lobe of the aedeagus (Seevers, 1978). In addition to these characteristics mentioned by Seevers, all members of the tribe Bolitocharini (except gyrophaenines, the maxillae of which are probably derived from similar structures) have a similar form of the maxilla. General characteristics of the bolitocharine maxilla are shown in Figures 96, 97 and 238. All bolitocharines have a lacinia with an acute tip, a short distal comb of more or less loosely scattered teeth, a subapical broadly protruded area densely covered with spines, teeth and setae, more scattered spines and teeth proximally along inner face, and entire inner face more or less densely covered with long scattered setae. Obviously, if the maxillae of gyrophaenines are derived from structures similar to these, the amount of modification required is extensive.

Although these similarities in structure are found among members of the Bolitocharini, which of these characteristics are actually autapotypies is unknown. All share the 4-4-5 tarsal formula. However, given Seevers' interpretation of the tribe Bolitocharini, a number of other tribes share this character. The 4-4-5 tarsal formula may be an autapotypy linking supertribal taxa. If so, it will be difficult to distinguish from parallel development of similar conditions.

The denticles on the molar surface of the mandibles are a more promising character. Mandibles of all bolitocharines that I have examined have denticles. Furthermore, they are lacking from most other aleocharines including members of tribes sharing the 4-4-5 tarsal formula with bolitocharines. Seevers (1978) suggested that these denticles on the mandibles may be associated with feeding on spores and hyphae of fungi. However, it is important to note that such denticles are not limited to bolitocharines. Seevers (1978) also reported similar denticles on the molar surface of members of the tribe Philotermitini, all of which are termitophilous. It is possible that this condition of the mandibles is independently derived in the philotermitines. However, this must be demonstrated, not assumed. In addition, a more complete survey of the mouthparts of aleocharines may show such mandibular denticles to be more widespread. No decision can be made about value of this character as an autapotypy for the Bolitocharini at the present time.

Usefulness of similarities in aedeagal structure in indicating the monophyletic nature of the Bolitocharini is uncertain. Seevers (1978: 161) described the median lobe of bolitocharines as

having a "difficult to define bolitocharine characteristic". Such ambiguity seems to indicate that one is dealing with an impression of general similarity rather than specific aedeagal characteristics. There are, however, a suite of characteristics in which the aedeagi of members of the Bolitocharini are more similar to each other than to those of most other aleocharines. The aedeagus of most members of the tribe Bolitocharini has a relatively simple median lobe with a oval, rather elongate, depressor plate; a large, more or less tubular flagellum which is slightly to moderately sclerotized in many; and an ejaculatory duct which extends the entire length of the flagellum, with the opening of the duct near the apex of the flagellum. In addition, the median lobe of most bolitocharines lacks complex internal structure and extensive eversible membranes armed with hooks and spines, as commonly found among aleocharines, and many of the aedeagal specializations found in other groups, such as the "athetine bridge" (Seevers, 1978) and the deep ventro-lateral incision of the basal bulb of the aedeagus. It is by no means clear which, if any, of these similarities in the median lobe of members of the Bolitocharini are true autapotypies. It is also important to note that if these similarities are part of the "ground plan" of the bolitocharine aedeagus, then modifications of this basic type have been extensive in some groups. Also, the characteristics mentioned above as shared among the bolitocharines may also be found in different combinations in other groups of aleocharines. Much more comparative study must be done on the detailed structure of the aedeagus of aleocharines before this group of characters can be evaluated.

The gyrophaenines do not share similarities in maxillary structure with other bolitocharines. For reasons discussed more fully below, it is here predicted that the highly specialized type of maxilla of gyrophaenines is derived from a type similar to that found among other bolitocharines.

In conclusion, it is apparent that the subtribe Gyrophaenina cannot be placed within the tribe Bolitocharini based on clearly polarized autapotypies. This, however, is a result of lack of knowledge of apotypic and plesiotypic states within the aleocharines rather than an inherent ambiguity in affinities of gyrophaenines. For the present, at least, affinities of any group of aleocharine must be based on "similarity" although it is quite possible to hypothesize apotypic conditions for the highly specialized states of structures or habits found in some groups of aleocharines. The gyrophaenines share more similarities with members of the tribe Bolitocharini than with any other group. Some of these similarities may be true autapotypies, but this hypothesis must await further study. In addition, the gyrophaenines, though highly specialized themselves, lack many of the specializations of other groups of aleocharines. For example, at present, it would be difficult to justify a hypothesis that members of the tribes Aleocharini, Falagriini and Athetini share a most recent common ancestor with gyrophaenines.

A hypothesis which must be considered is that gyrophaenines form the sister group to the entire tribe Bolitocharini, rather than being included within it. The gyrophaenines are certainly highly autapotypic in some characters in relation to other members of the Bolitocharini. However, the remainder of the Bolitocharini as a group do not seem to have autapotypies not found in gyrophaenines. Elevation of gyrophaenines to tribal rank because of their highly specialized habits would make the Bolitocharini paraphyletic. While paraphyletic groups can be justified, I will argue below that some evidence suggests that gyrophaenines share their closest common ancestor with members of a subtribe within the Bolitocharini. This relationship is best emphasized by ranking the gyrophaenines as the subtribe Gyrophaenina within the tribe Bolitocharini.

The subtribe Bolitocharina as considered here is essentially equivalent to the group "Bolitocharae" of Seevers (1978). I differ with his interpretation of the subtribe in that I question whether *Leptusa* Kraatz should be included. All members of *Leptusa* have very narrowly separated or contiguous middle coxae, and the intercoxal processes are short with a relatively long, narrow isthmus. In addition, the median lobe of males of *Leptusa* is quite different from that found in most other bolitocharines. I also question Seevers' synonymy of all of Casey's generic names within this subtribe with the European *Bolitochara* Mannerheim. Having seen specimens of all of Casey's genera, I agree that they are almost certainly related to *Bolitochara*, but they differ substantially from specimens of that genus and among themselves, and at least some of Casey's genera are probably valid. It will take considerable study of relationships within the tribe Bolitocharini to solve this problem. However, the differences in interpretation of the subtribe Bolitocharina used here, and Seevers' group "Bolitocharae" (except perhaps for the position of *Leptusa*) does not seriously affect the possible hypotheses about relationships.

Members of both the Bolitocharina and Gyrophaenina have those similarities discussed above shared by other members of the tribe Bolitocharini. In addition, they are also similar in the following characteristics (Figure 251): 1) both have middle coxae which are widely divided by processes from the meso- and metasternum (very widely divided in all gyrophaenines, presumably secondarily narrowed in many bolitocharines); 2) mesosternal process which extends to near middle or just posterior to middle of coxae (assumes character 36 is correctly polarized for the plesiotypic condition for gyrophaenines); 3) a relatively short isthmus (absent from gyrophaenines); 4) mouthpart structure (particularly maxillae) similar, in that both the bolitocharine type and the gyrophaenine type can be derived from a common ancestor; and 5) similar patterns of micro- and macrosetae. It is probably also important that members of both these subtribes are associated with fresh mushrooms or fungi. The gyrophaenines are obligatorily mycophilous and mycophagous. Less is known about the habits of bolitocharines, and their precise relationship to fresh fungi has not been carefully studied. It is apparent from mouthpart structure that bolitocharines are not as highly specialized as fungus-feeders as are gyrophaenines, but they are almost certainly at least facultatively mycophagous.

Although it is not a logical necessity that the sister group of gyrophaenines also be associated with fungi, the most recent common ancestor of gyrophaenines and their sister group must have had mycophilous habits. It would, therefore, not be surprising if the sister group of gyrophaenines was also associated with fresh fungi. In mouthpart structure and habits, members of the subtribe Bolitocharina satisfy most of the characteristics which might be predicted for the plesiotypic sister group of the gyrophaenines.

Again, it is impossible to be certain which of the characteristics shared by bolitocharines and gyrophaenines are true autapomorphies. However, gyrophaenines do not share a similar suite of characters with any other group of aleocharines.

Mycophily and mycophagy are certainly highly derived conditions among aleocharines. However, the mycophilous habits of members of these two subtribes may be parallel modifications in response to a similar habitat. While this is a possibility, the hypothesis that mycophily in these two subtribes is derived from a common ancestor with mycophilous habits can be falsified only by showing that either the bolitocharines or the gyrophaenines share at least one well established apomorphy with some third group of aleocharines not shared by the other subtribe. At the present state of knowledge, no such autapomorphy is known. A sister group relationship between Bolitocharina and Gyrophaenina seems to be a reasonable hypothesis

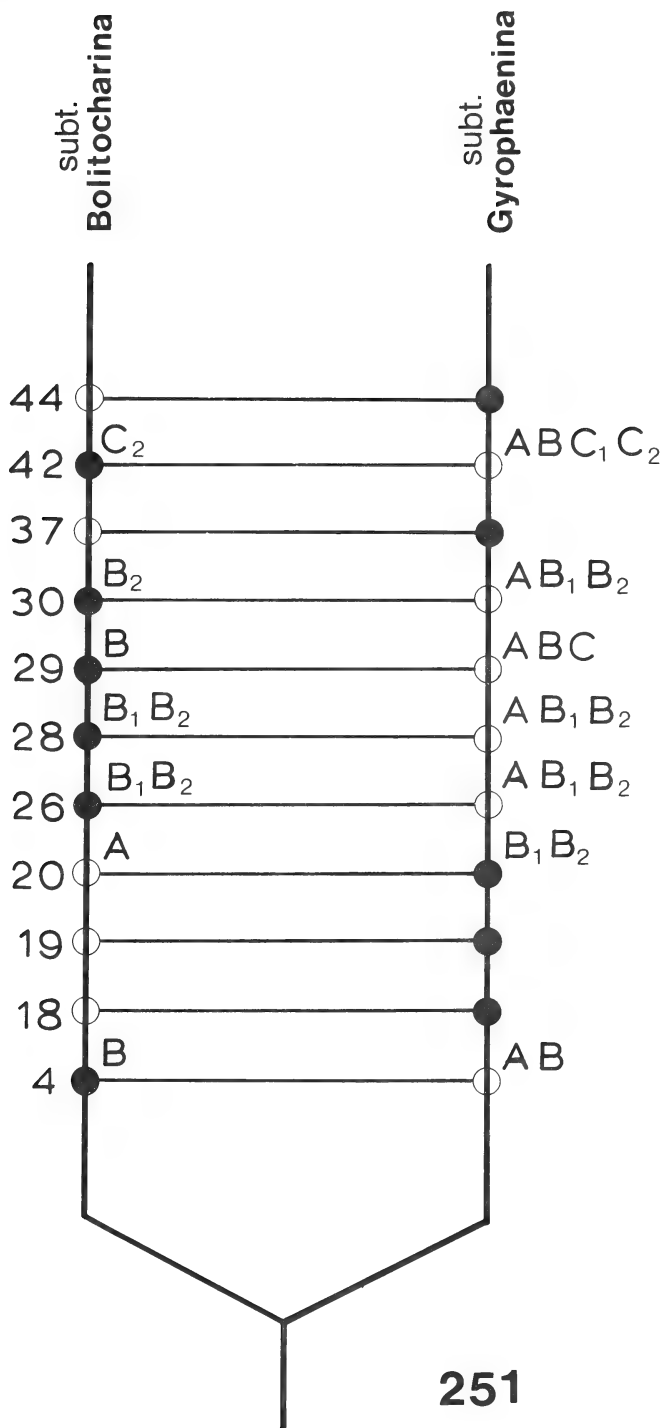


Figure 251. Hypothesized cladistic relationships between subtribes Bolitocharina and Gyrophaenina.

(Figure 251).

The bolitocharines have become longer, narrower insects. This is reflected in the less transverse shape of the pronotum. Derived states of Characters 26, 28, 29 and 30 are an integrated system relating to this narrowing. These characteristics are developed in parallel in the "*Gyrophæna*" lineage of gyrophænines. In addition, the bolitocharines have modified the setose area on Tergum 10 to a chevron-shaped area (42 C).

Most modifications in gyrophænines have apparently been in response to increased mycophagy and involve development of the spore brush of the maxilla. These modifications of the maxilla include 1) truncation of the apex of the lacinia; 2) increase in number and density of teeth on truncated area of lacinia; and 3) decrease in number of teeth and spines on inner face of lacinia as the manipulative function of the inner face decreases. Additional modifications within the Gyrophænina are discussed below.

The hypothesis that members of the subtribe Gyrophænina as considered here constitute a monophyletic group is supported by at least two strong autapotypies: 1) modification of the maxilla as a spore gathering structure; and 2) presence of a lateral plate on the neck of the spermatheca. Modification of the maxilla is an integrated complex of characters. In the most plesiotypic condition known among gyrophænines, this complex involves modifications of the apex of the lacinia from acute to obliquely truncate (18 B), increase in number and density of lacinial teeth (19 B), and reduction of number of teeth and spines on the inner face of the lacinia (20 B). Further modifications of this structure within the gyrophænines reflect increased specialization for feeding on the hymenium layer of mushrooms.

A lateral plate on the neck of the spermatheca (44 B) characterizes females of all gyrophænines examined. Although the structure of the spermatheca has not been well investigated, no similar structure is known to occur in any other group of aleocharines. This lateral spermathecal plate is almost certainly a uniquely derived character state within the gyrophænines and, as such, provides strong evidence that they form a monophyletic group.

Structure of the maxilla of gyrophænines is unlike any other known among aleocharines. Because all known gyrophænines are obligatory mycophages, it is a reasonable possibility that this maxillary structure represents parallel modifications for fungus feeding in two or more aleocharine lineages. However, two things support the hypothesis that the similarity is an autapotypy. As noted above, the modification for spore feeding actually involves a complex of characters. That such a large group of characters would be indistinguishably modified in parallel in two or more distantly related lineages seems unlikely. Secondly, as far as presently known, congruence between maxillary modifications and presence of the lateral spermathecal plate in females is universal among gyrophænines. Therefore, mouthpart structure is best interpreted as a uniquely derived character within the gyrophænines.

The hypothesis that contiguous mesosternal and metasternal processes (37 B) is an apotypy for the subtribe Gyrophænina is dependent on the assumption that a slight isthmus in members of *Agaricochara* is secondarily derived. This seems reasonable because of the uniformity of the derived condition among all other gyrophænines.

While specimens of *Probrachida* and *Brachida* have apotypic states of many characters, they are quite primitive, particularly their mouthparts. Specimens of *Probrachida* have the most plesiotypic mouthparts among gyrophænines.

These two lineages likely diverged early in phylogeny of gyrophænines, but their exact relationships are problematical, because it is difficult to place *Brachida*. Because of the plesiotypic character states retained by *Probrachida*, it is apparent that this group must occupy



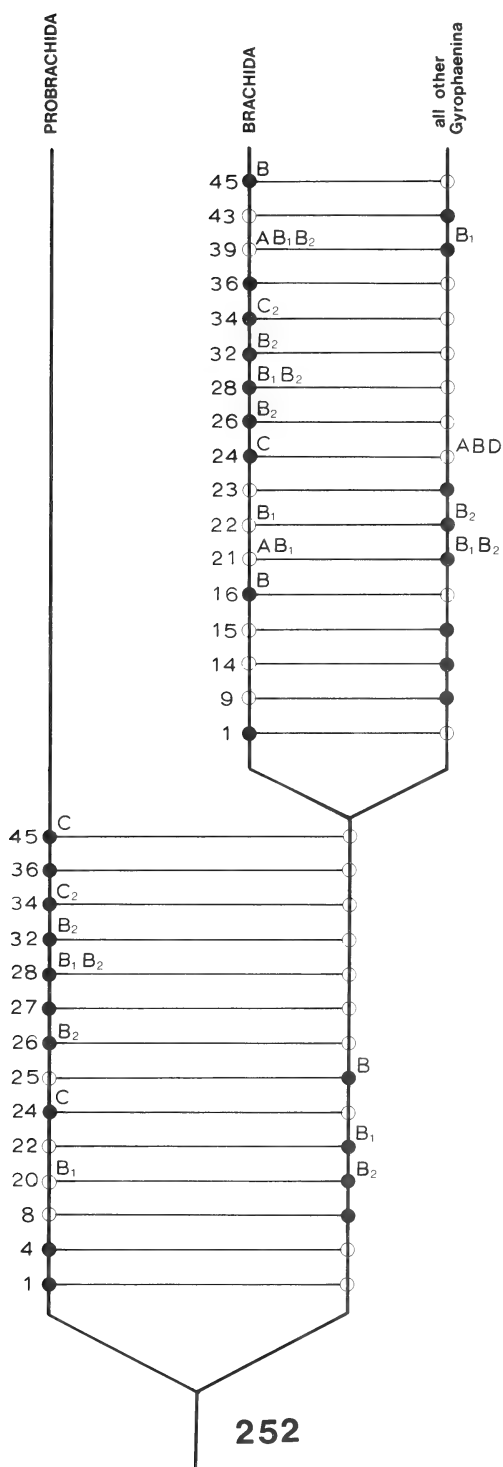


Figure 252. Hypothesized cladistic relationships among *Probrachida*, *Brachida* and all other *Gyrophaenina*, Hypothesis I.



a basal position in any reconstructed phylogeny of known extant gyrophaenines. In contrast, the position of *Brachida* can be reasonably interpreted in two ways. Alternatives are depicted in Figures 252 and 253.

In the Hypothesis I (Figure 252), *Probrachida* is considered to be the sister group to all other gyrophaenines including *Brachida*, and within this group *Brachida* is sister to the remainder. The principal assumptions are that loss of teeth from the inner face of the lacinia (20 *B*<sub>2</sub>) and reduction of medial setae of the labium from two to one (25 *B*<sub>1</sub>) has occurred only once among gyrophaenines.

Under this hypothesis, the lineage which led to *Probrachida* is characterized by ten apotypic character states as opposed to hypothetical states of these characters in the ancestor of the "*Brachida* and all other gyrophaenines" lineage, and retains four plesiotypic character states in relation to all other gyrophaenines (Figure 252).

Members of the lineage "*Brachida* and all other gyrophaenines" share five apotypic states.

*Brachida* is characterized by nine apotypic states. Furthermore, members of *Brachida* retain eight plesiotypic states relative to all other gyrophaenines (Figure 252).

Hypothesis I is weakened by the requirements of parallel development of apotypic states in six characters in *Probrachida* and *Brachida*: 1 *B*<sub>1</sub>, 16 *B*, *C*, 24 *C*, 28 *B*<sub>1</sub>, *B*<sub>2</sub>, 32 *B*<sub>2</sub>, 34 *C*<sub>2</sub>, and 36 *B*. In addition, this hypothesis implies that the pair of medial macrosetae on the head are independently lost from *Probrachida* (4 *B*); some species of *Brachida* have independently evolved antennomere 4 similar to 5-10 (8 *A*); and some *Brachida* have independently evolved spatulate setae on the galea (23 *B*).

Hypothesis II (Figure 253) considers *Probrachida* and *Brachida* sister groups, with the two together forming the sister group to the remaining extant gyrophaenines. The principal assumption of this hypothesis is that the broad, undivided ligula is a synapotypy between *Probrachida* and *Brachida*. Under this hypothesis these genera share eight apotypic character states. In addition, members of this lineage retain ten plesiotypic character states not found among other gyrophaenines (Figure 253).

If *Probrachida* and *Brachida* form a monophyletic group, then parallel evolution of apotypic states of a number of characters between members of this lineage and other gyrophaenines is required. If antennomere 4 similar to 5-10 (8 *A*) is plesiotypic for this lineage, then modification of antennomere 4 to be similar to 1-3 (8 *B*) must have occurred independently in some species of both *Probrachida* and *Brachida*, and in the ancestor of all other gyrophaenines. Teeth on the inner face of the lacinia (20 *B*<sub>1</sub>) in members of *Probrachida* suggests that members of the ancestor of *Probrachida* and *Brachida* must have had this condition. If so, loss of these teeth (20 *B*) must have occurred independently in *Brachida* and the ancestor of all other gyrophaenines. If numerous scattered setae on the inner face of the lacinia (21 *A*) is plesiotypic for the lineage, then reduction in number (21 *B*) must have occurred independently in some species of *Probrachida*, *Brachida* and the ancestor of the remaining gyrophaenines. Similarly, reduction of number of setae on the inner face of the lacinia to a single row must have occurred independently in some species of *Brachida* and a number of other gyrophaenine lineages; reduction in number of rows of setae on the galea (22 *B*<sub>1</sub>, *B*<sub>2</sub>) in *Probrachida*, *Brachida* and the ancestor of the other gyrophaenines; and modification of these setae to plate-like structures (23 *B*) in a few species of *Brachida* and the ancestor of the other gyrophaenines. In addition, two medial setae on the labium (25 *A*) of all members of *Probrachida* suggest that the ancestor of *Probrachida* and *Brachida* must have had this

condition. If this is so, then reduction to one such seta occurred in both *Brachida* and the ancestor of all other gyrophaenines. Finally, reduction in number of setae on the metepisternum to two irregular rows (39  $B_1$ ) or a single well defined row (39  $B_2$ ) must have occurred in species of *Brachida* as well as in several other lineages.

Hypothesis II is weakened in particular by the requirement of independent evolution of character states 20  $B_2$ , 21  $B_2$ , and 25  $B$ , in at least some species of *Brachida* and the ancestor of the remaining gyrophaenines. However, based solely on number of required parallel evolutionary modifications, this is a more parsimonious hypothesis than Hypothesis I. Also, the lineages of both *Probrachida* and *Brachida* can be derived from an ancestor having a number of relatively plesiotypic character states in relation to the ancestor of the other gyrophaenines. Presence of some species in both *Probrachida* and *Brachida* which have plesiotypic character states and others which have apotypic states suggests that parallelism, probably in response to similar habit, is common.

These considerations lead me to accept Hypothesis II, given the present state of knowledge.

The *Probrachida-Brachida* lineage is arbitrarily and informally designated the "*Brachida*" lineage.

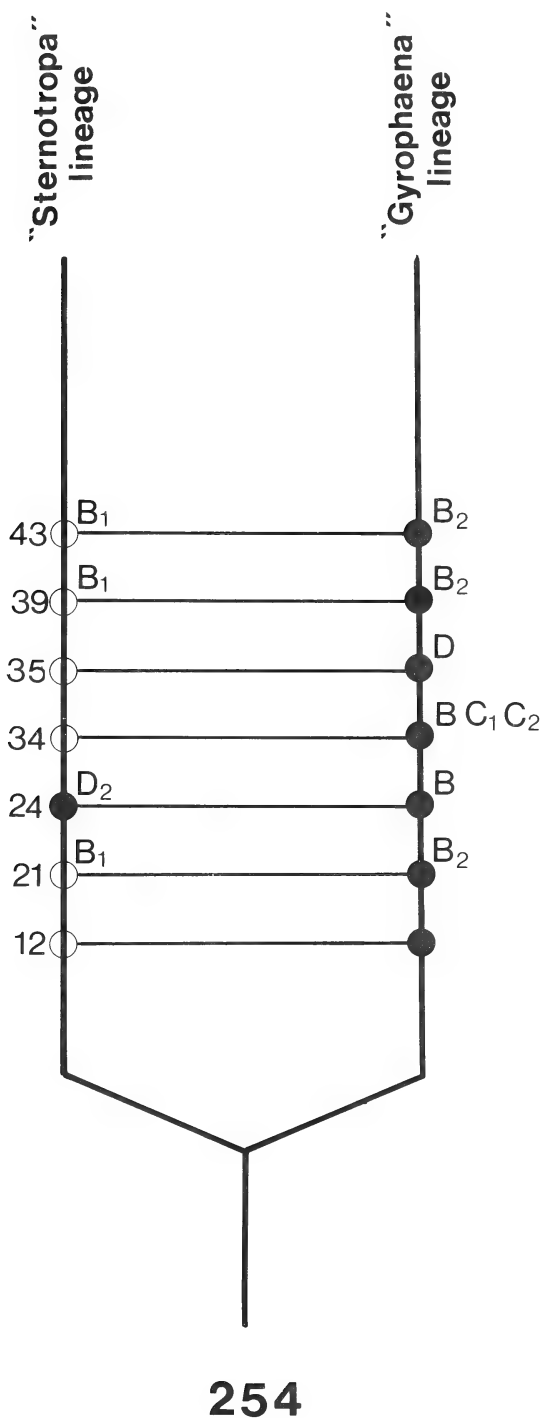
Members of the "*Brachida*" lineage retain a number of plesiotypic conditions found in no other gyrophaenines. In particular, the retention of teeth and numerous, scattered setae on the inner face of the lacinia, and numerous rows of unmodified, filiform setae on the apex of the galea of *Probrachida*, are the most plesiotypic conditions of maxillary structures found in known gyrophaenines.

Within the "*Brachida*" lineage, both *Probrachida* and *Brachida* are hypothesized to be monophyletic lineages based on autapotypic states of several characters (Figure 253). In addition, specimens of each genus have distinctive ground plans for the median lobe of the aedeagus. These two basic aedeagal types may have been derived from that found in a common ancestor. However, the type found in males of *Brachida* is extremely aberrant in relation to that found among other gyrophaenines (see discussion under this genus), and it seems unlikely that it would have been derived from an ancestral type very similar to that found in males of *Probrachida*. It seems most reasonable to hypothesize that, in many characters, males of *Probrachida* and *Brachida* are each derived in relation to a common ancestor.

The group made up of the "*Sternotropa*" and "*Gyrophaena*" lineages contains most of the species in the subtribe. Within the ancestor of these lineages, most of the highly derived characteristics typical of adaptation of gyrophaenines for an intimate association with fresh mushrooms must have developed.

Ten strong autapotypies support the hypothesis that the members of the "*Sternotropa*" and "*Gyrophaena*" lineages together form a monophyletic group (Figures 253, 254). In addition, distribution of character states within the "*Sternotropa*" and "*Gyrophaena*" lineages suggests that the common ancestor must have retained states of a number of characters which are plesiotypic for the gyrophaenines as a whole. These include: 1  $A$ , 16  $A$ , 26  $A$ , 28  $A$ , 29  $A$ , 30  $A$ , 32  $A$ , 33  $A$ , 34  $A$ , 35  $A$ , 36  $A$ , 38  $A$ , and 45  $A$ .

Concordance of apotypic states in mouthpart characters (particularly 20  $B_2$ , 21  $B_1$ , 23  $B$ , and 25  $B_1$ ) in all species of these two lineages is strong evidence for monophyletic origin of the "*Sternotropa*" and "*Gyrophaena*" lineages. As discussed earlier, because all members of these lineages are, as far as is known, obligatorily mycophagous on fresh mushroom fruiting bodies, there is the possibility of parallel development in mouthpart structure. However, to date the known apotypic states of these characters are congruent among all members. That



254

Figure 254. Hypothesized cladistic relationships between "Sternotropa" and "Gyrophaena" lineages.

indistinguishably similar apotypies could be derived independently in many characters seems a less parsimonious hypothesis than that all were developed in the same ancestor. To falsify the hypothesis that these two lineages form a monophyletic group would require that variation be found in the shared apotypies listed above (particularly in mouthparts) which would indicate that they were developed in parallel. In addition, if new strong apotypies are found which are incongruous with apotypic states of the mouthpart characters, it would suggest that similarity in mouthpart structure may have evolved in response to similar habits rather than derivation from a common ancestor.

The "*Sternotropa*" lineage (Figure 255) is comprised of the genera *Sternotropa* Cam., *Pseudoligota* Cam., *Adelarthra* Cam., *Agaricomorpha* n.gen., *Brachychara* Shp., and *Neobrachida* Cam. In addition, the most parsimonious cladistic placement of *Agaricochara* Kraatz is in this lineage. These seven genera (with the possible exception of *Agaricochara*) appear to have a monophyletic origin.

The principal assumption in the hypothesis of a monophyletic origin for this group is that the deeply bifid ligula has been derived only once in the gyrophaenines. It is important that the bifid ligula (24  $D_1$ ,  $D_2$ ,  $E$ ) is the only apotypy shared by all members of the "*Sternotropa*" lineage. Similarity of this structure in members of *Sternotropa*, *Pseudoligota*, *Agaricomorpha* and *Brachychara* provides evidence that the bifid ligula is of monophyletic origin at least in these groups. However, variation in detailed structure of the bifid ligula, particularly in the rather robust lobes of the ligula in specimens of *Adelarthra*, the elongate apically bifid ligula of specimens of *Neobrachida*, and the slightly divided ligula of *Agaricochara* species, suggests that bifurcation may have occurred more than once among the gyrophaenines. Also, all members of the "*Sternotropa*" lineage for which natural history information is available are inhabitants of woody polypores. Therefore the hypothesis that a bifid ligula may in some way be associated with living or feeding on polypores is a distinct possibility.

The possibility that the bifid ligula has been derived more than once is especially serious because of lack of strong apotypic states of other characters in members of this lineage. Additional apotypic states might show congruence or discordance with distribution of the bifid ligula and would provide a test for hypotheses about the monophyletic origin of this character state.

Members of the "*Sternotropa*" lineage are all very similar in general body form. However, this similarity is best interpreted as the result of symplesiotypy, as discussed below.

Modification of the setal patch on Tergum 10 to an inverted-V or chevron-shaped patch (or distinct rows) (42  $C_1$ ,  $C_2$ ) in most of the species in this lineage may be taken as an additional apotypy for this lineage. However, presence of a square setal patch (42  $B$ ) in some species suggests that the ancestor of the "*Sternotropa*" lineage had a square patch. This tendency to form a chevron-shaped patch may be an "underlying synapotypy" (Saether, 1979). It is impossible to distinguish between true underlying synapotypies (reflecting genetic similarity) and parallelisms resulting from strong selection pressure for similar features. The chevron-shaped patch on Tergum 10 has been derived so commonly among members of this lineage that it is tempting to suggest some underlying genetic similarity among these insects. However, it is also important to remember that they all appear to live in a similar habitat, polypore mushrooms.

*Neobrachida* and *Adelarthra* show variation in structure of the bifid ligula, but share apotypic conditions of several characters (discussed more fully below) with some other members of the "*Sternotropa*" lineage. This provides additional evidence that they are

members of this lineage, and that the bifid ligula is actually an autapotypy among members of this lineage.

*Agaricochara* is tentatively placed in this lineage by the slightly divided ligula. However, members of this genus share a number of similarities with the "*Gyrophaena*" lineage. Therefore, alternative hypotheses about the position of *Agaricochara* within the cladogram may be postulated. These alternatives are discussed more completely below, but since the bifid ligula is the only apotypy shared by *Agaricochara* with other members of the "*Sternotropa*" lineage, it provides no additional information about the origin of this character state.

In spite of problems with this character, because of present lack of evidence to the contrary, I accept the hypothesis that the bifid ligula is uniquely derived in the ancestor of the "*Sternotropa*" lineage. However, the monophyly of this lineage is not markedly established, and a search for additional character states which will support or negate this hypothesis is needed.

The "*Sternotropa*" lineage is particularly characterized by retention of plesiotypic states of nine characters in most species of the lineage (Figure 255). Common retention of plesiotypies, in addition to a large percentage of the members of the "*Sternotropa*" lineage being small to very small, dark, slightly limuloid beetles, densely covered with short microsetae, give the members of this group a rather uniform appearance. Such similarity in a large number of character states among members of a group, all of which appear to occupy a similar habitat, suggests the possibility that these character states are similarities derived in response to a common environmental stimulus, and thus are apotypies rather than plesiotypies. However, neither in-group nor out-group comparisons support this hypothesis (see character analysis above). Until additional evidence encourages re-evaluation of character analysis and polarities within the gyrophaenines, it seems most reasonable to hypothesize that general similarity in habitus among members of the "*Sternotropa*" lineage is mostly due to widespread retention of plesiotypies.

The cladistic relationship of *Agaricochara* within the gyrophaenines is uncertain. As indicated above, two hypotheses can be reasonably proposed at the present time. The monophyletic lineage which led to *Agaricochara* may have originated soon after origin of the "*Sternotropa*" lineage; if so, it is the sister group to all remaining members of this lineage (Figure 255). Alternatively, it may have originated near the base of the "*Gyrophaena*" lineage (Figure 259). Neither of these hypotheses is markedly supported. If the hypothesis that *Agaricochara* is a member of the "*Sternotropa*" lineage is accepted, then it is a highly autapotypic member. In particular, in the apotypic states of this genus, it shows a great deal of parallelism with members of the "*Gyrophaena*" lineage. Apotypic character states present among members of *Agaricochara* shared in parallel with the base of the "*Gyrophaena*" lineage include 34 *B* and 39 *B*<sub>2</sub>. Characters shared in parallel with some members of the "*Gyrophaena*" lineage but not found in any other member of the "*Sternotropa*" lineage include 28 *B*<sub>1</sub>, 30 *B*<sub>1</sub>, 34 *C*<sub>1</sub>, and 40 *B*. State 40 *B* is shared with a few members of the "*Sternotropa*" lineage.

Placement of *Agaricochara* within the "*Sternotropa*" lineage is very tentatively accepted in this study. Most of the apotypic character states that members of *Agaricochara* share with members of the "*Gyrophaena*" lineage are either reductions or likely to be subject to parallelism (see discussion under "*Gyrophaena*" lineage). However, evidence for this conclusion is weak and contradictory, and considerable additional study of relationships of members of this genus is required to more confidently place it among the gyrophaenines.

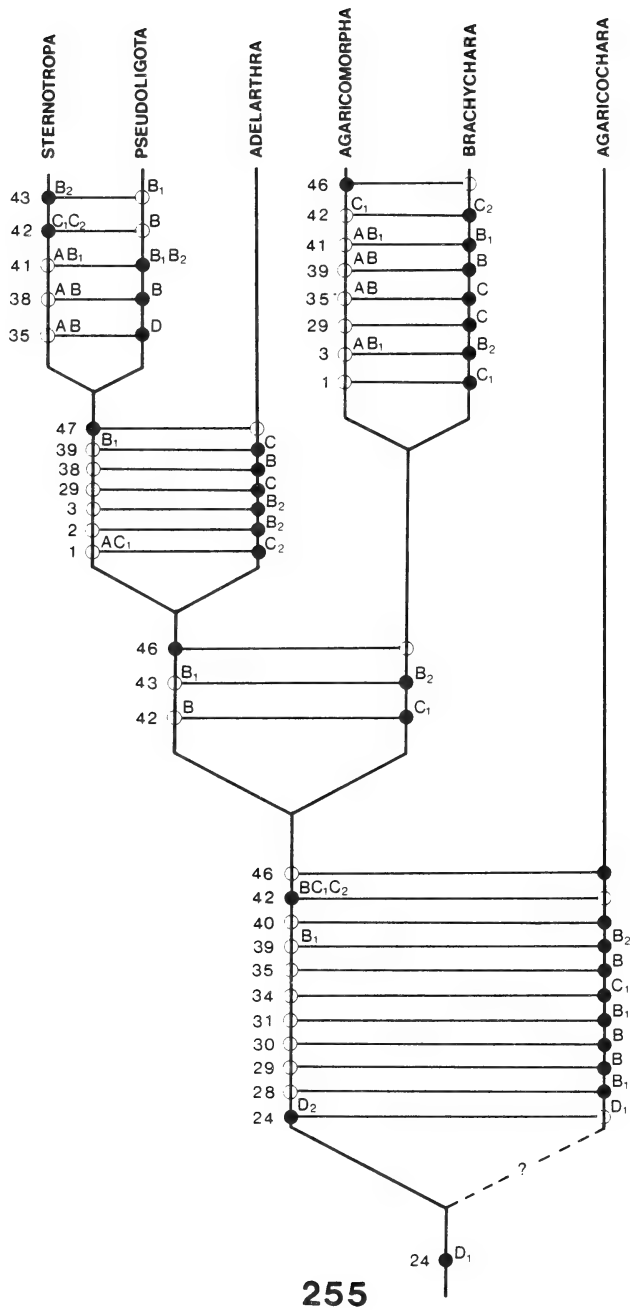


Figure 255. Hypothesized cladistic relationships among members of the "Sternotropa" lineage.



The remainder of the "*Sternotropa*" lineage is hypothesized to form a monophyletic group on the basis of common possession of a deeply divided ligula (24  $D_2$ ). The elongate apically divided ligula of *Neobrachida* is probably an autapotypic condition within this lineage. This portion of the "*Sternotropa*" lineage is naturally divided into two monophyletic lineages: 1) a lineage including *Sternotropa*, *Pseudoligota*, *Adelarthra* and tentatively *Neobrachida*; and 2) a lineage including *Agaricomorpha* and *Brachychara*.

The grouping made up of *Sternotropa*, *Pseudoligota* and *Adelarthra* (Figure 255) is hypothesized to be monophyletic based on the common possession by males of a highly autapotypic condition of the median lobe of the aedeagus (46). This aedeagus type is characterized by origin of a long filiform flagellum near the basal bulb. In most species the flagellum forms a loop proximally around the basal bulb and is extended distally in a groove in the functionally ventral surface of the aedeagus. This aedeagus type is very distinctive and is found in no other group within the Gyrophaenina. It appears to be strong evidence that this is a monophyletic group.

In comparison to the sister lineage of the group, the ancestor of *Sternotropa*, *Pseudoligota* and *Adelarthra* must have retained several plesiotypic states including 42  $B$ , and 43  $B_1$ .

Within this lineage, *Sternotropa* and *Pseudoligota* are hypothesized to be sister lineages based on common possession of the characteristic type of aedeagal median lobe described above, and also by autapotypic conditions of the parameres (Character 47). In males of both genera, two of the setae of the apical sclerite of the parameres are located far toward the base of the sclerite, and are disproportionately large (Figures 227, 229).

Within the lineage *Sternotropa*-*Pseudoligota*, *Sternotropa* is hypothesized to be monophyletic based on common possession by members of this genus of two autapotypic character states, and monophyly of *Pseudoligota* is supported by presence of three autapotypic character states.

*Adelarthra* is a highly autapotypic member of this monophyletic group of genera, and its relationship to *Sternotropa* and *Pseudoligota* is uncertain. To properly evaluate character state distribution among these genera, three hypotheses are considered (Figures 256A-C). Hypotheses I and II are dependent on whether a fused suture between the meso- and metasternal processes (38  $B$ ) is an autapomorphy among members of *Pseudoligota* and *Adelarthra*, or whether it has evolved in parallel in these two genera.

Hypothesis I (Figure 256A) is based on the assumption that fused meso-metasternal processes have been evolved in parallel in the ancestors of these genera. In this situation, there is no synapomorphy uniquely shared by members of any pair of genera. Postulation of an unresolved trichotomy is unavoidable. In hypothesis II (Figure 256B) it is assumed that the presence of a fused meso-metasternal process is uniquely derived by the ancestor of *Pseudoligota* and *Adelarthra*, with these two genera as the sister group to *Sternotropa*. The sister group relationship between *Pseudoligota* and *Adelarthra* is, however, very inadequately supported by this character state (38  $B$ ) because of the possibility of indistinguishable parallel development of the apotypic state. In this regard, it is important to note that members of a number of species of *Sternotropa* have independently evolved the fused condition, suggesting that parallelism in this character is common.

If, however, structure and position of the setae on the apical sclerite of the parameres of males of *Pseudoligota* and *Sternotropa*, as described above, is considered uniquely characteristic in members of these two genera, then Hypothesis I is transformed into Hypothesis III. Hypothesis III (Figure 256C) states that *Adelarthra* is the sister group to

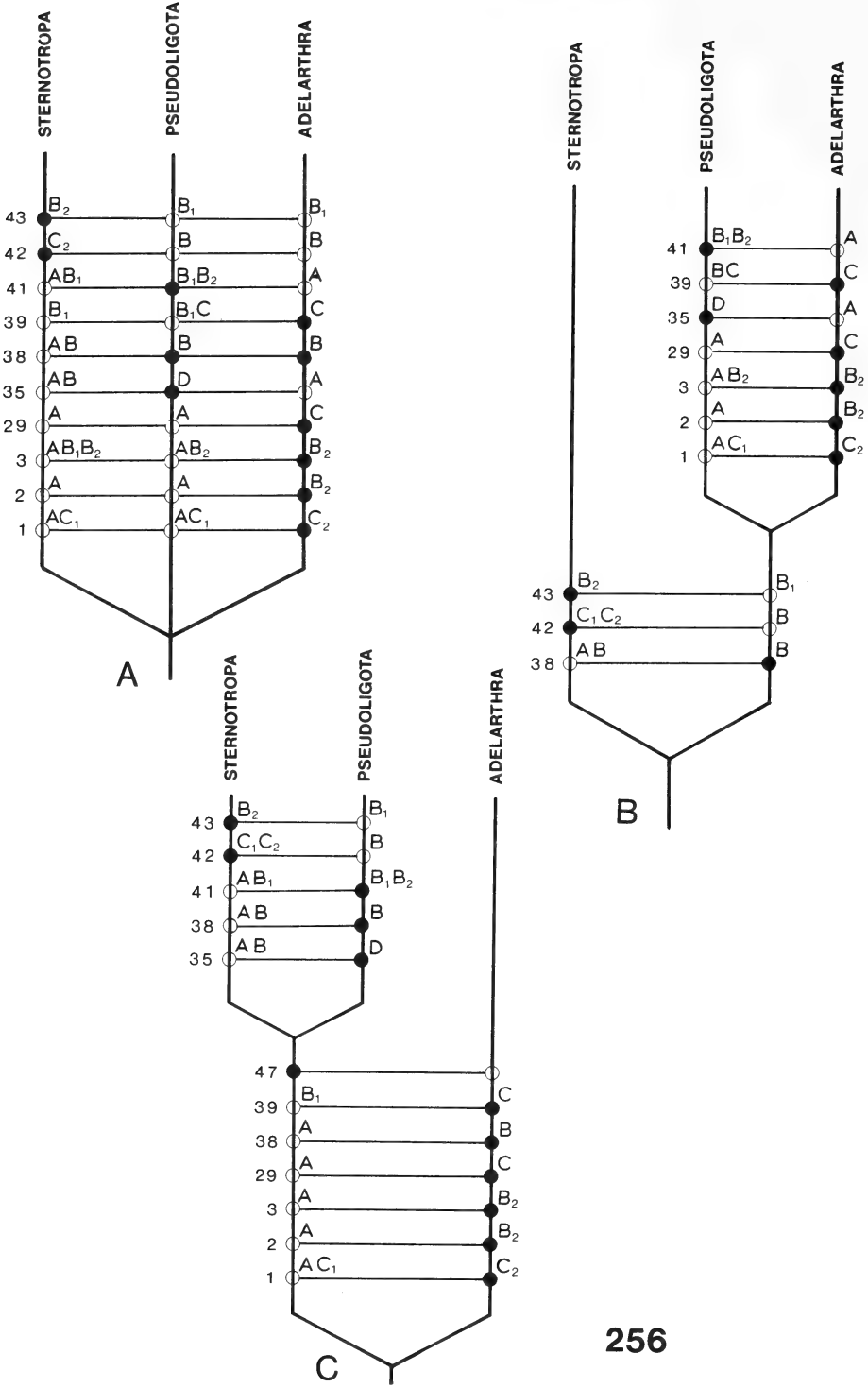


Figure 256. Possible cladistic relationships of *Adelarthra* Cam. A) Hypothesis I. B) Hypothesis II. C) Hypothesis III.

*Pseudoligota* plus *Sternotropa*. This hypothesis is no more parsimonious than Hypothesis II based on number of shared apotypic characters, but Hypothesis III is more likely to be correct because the apotypic condition of the parameres shared by males of *Sternotropa* and *Pseudoligota* is less likely to have been derived in parallel than is the fused state of the intercoxal processes shared by *Pseudoligota* and *Adelarthra*. Therefore, I tentatively accept Hypothesis III as presently the most likely of the possible cladistic relationships between *Adelarthra*, *Sternotropa* and *Pseudoligota*. Under this hypothesis, *Adelarthra* is highly autapotypic in six characters when compared to members of its sister lineage.

The cladistic relationships of *Neobrachida* are the most inadequately understood of any known group within the "*Sternotropa*" lineage. This is, in large part, a result of the fact that no specimens of this genus are available for detailed examination, and no males are known. Therefore, structure of the mouthparts is virtually unknown, and nothing is known of the aedeagus or spermatheca. The hypothesis presented in Figure 257 is based on the assumption that the chevron-shaped setal patch on Tergum 10 (42  $C_1$ ) and flattened, subspatulate setae on this sclerite (43  $B_2$ ) are shared derived characters between *Neobrachida* and *Sternotropa*. However, this relationship is very weakly founded. Since neither aedeagus nor spermatheca are known, it is not known whether members of *Neobrachida* share the unique aedeagus type of *Sternotropa* and related genera. Therefore, *Neobrachida* may not be related to this group of genera. In addition, structure of the ligula in *Neobrachida* is quite aberrant in relation to other members of the "*Sternotropa*" lineage.

Alternative placements of this genus include: 1) *Neobrachida* as sister group to *Sternotropa* plus *Pseudoligota*, implying independent derivation of the chevron-shaped setal patch (42  $C_1$ ) and subspatulate setae (43  $B_2$ ) in *Sternotropa* and *Neobrachida*; and 2) *Neobrachida* as the sister group to *Sternotropa* plus *Pseudoligota* plus *Adelarthra*, implying the same parallel developments. Neither of these placements can presently be supported by shared apotypic character states. Little more can be done with the cladistic relationships of *Neobrachida* at present.

The pair of genera *Agaricomorpha* and *Brachychara* is hypothesized to form a monophyletic group (Figure 255) on the basis of two shared character states (42  $C_1$  and 43  $B_2$ ). The uniform distribution of apotypic states of these two characters among members of *Agaricomorpha* and *Brachychara* contrasts with plesiotypic states of these same characters in many species of the *Sternotropa*-*Pseudoligota*-*Adelarthra* group of genera. This indicates that the ancestor of *Sternotropa* and related lineages must have had the plesiotypic state of these characters, while the ancestor of *Agaricomorpha* and *Brachychara* must have had the apotypic state and supports the hypothesis that these two groups of genera are sister groups.

Only a single autapotypy supports the hypothesis that *Agaricomorpha* is monophyletic and has a sister-group relationship with *Brachychara*. In males of all members of *Agaricomorpha* examined, the apical lobe of the median lobe of the aedeagus is displaced laterally (Figures 215A, B), not otherwise known among the gyrophaenines. It is, therefore, hypothesized to be uniquely derived within this lineage. In other characters, *Agaricomorpha* is markedly plesiotypic in relation to *Brachychara*. If additional study should indicate that the aedeagus type described above is plesiotypic rather than apotypic, or, if it has been derived within some lineage of *Agaricomorpha* rather than in its common ancestor, then *Agaricomorpha* would have to be considered paraphyletic in relation to *Brachida*.

In constast, members of *Brachychara* are markedly autapotypic and the monophyly of this lineage is well supported by seven apotypic features (Figure 255). The possible hypothesis that

members of this genus may be only a highly autapotypic lineage of *Agaricomorpha* cannot be conclusively rejected because of lack of clear knowledge of polarity in aedeagal characters. However, the median lobe of males of *Brachychara* does not have the laterally displaced apical lobe characteristic of males of *Agaricomorpha*. This suggests that the ancestor of both groups had a more generalized aedeagus than that found in *Agaricomorpha*, and supports the hypothesis that these are sister groups.

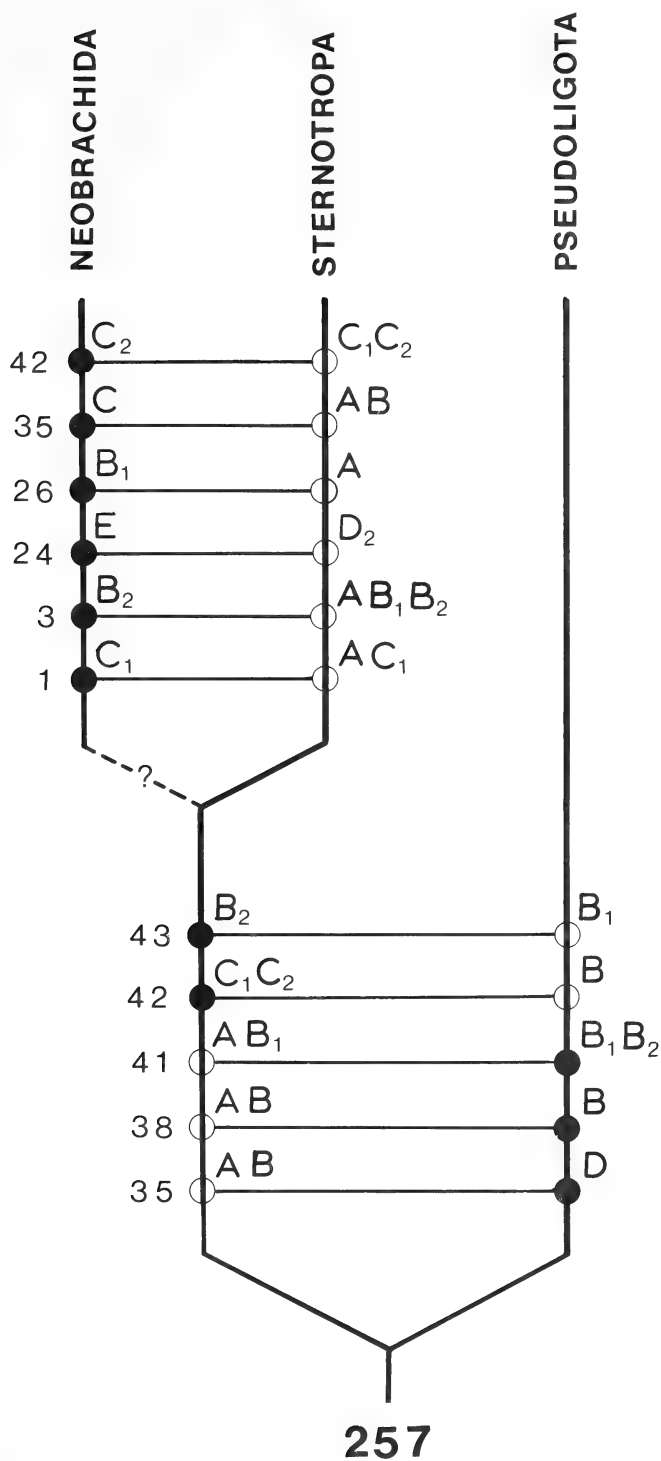
The "*Gyrophæna*" lineage is comprised of three genera: *Phanerota* Casey, *Eumicrota* Casey, and *Gyrophæna* Mannerheim (Figure 258). Structural evidence supports the hypothesis that these three genera have a monophyletic origin. In addition, some evidence suggests that *Agaricochæra* may be a member of this group. However, as discussed above, *Agaricochæra* may also be interpreted to be a member of the "*Sternotropa*" lineage.

No single strong apotypy supports the hypothesis that the "*Gyrophæna*" lineage forms a monophyletic group. Instead, there are a number of moderately useful to relatively weak derived character states shared in concordance by members of this lineage. Most important among these hypothesized apotypies is the undivided, protruded ligula (24 *B*) characteristic of all members of the lineage. If this is actually a derived condition of the ligula among gyrophaenines, then it offers strong support that these genera have a monophyletic origin. However, as discussed in the character analysis, this character state may also be interpreted as most similar to the character state from which the ligula type of other gyrophaenines was derived. If so, then common possession of this character state would provide no evidence about cladistic relationships. As indicated in the character analysis, at present the simple protruded ligula is not easily interpreted as an apotypic condition within the gyrophaenines. Nevertheless, even if this character state is interpreted as plesiotypic within gyrophaenines, it does not seriously affect the hypothesis that the "*Gyrophæna*" lineage is monophyletic. In addition, five other apotypic character states are shared by members of the "*Gyrophæna*" lineage in contrast to the "*Sternotropa*" lineage.

In comparison to the "*Sternotropa*" lineage, members of the "*Gyrophæna*" lineage form a very diverse assemblage. The distribution of hypothesized plesiotypic conditions among members of this lineage suggests that the ancestor of the "*Gyrophæna*" lineage must have retained the following plesiotypic conditions: 1 *A*, 3 *A*, 28 *A*, 29 *A*, 30 *B*<sub>1</sub>, *B*<sub>2</sub>, 32 *A*, 33 *A*, 36 *A*, and 42 *A*. In addition, given the remarkable diversity of basic aedeagal forms within the "*Gyrophæna*" lineage, the ancestor must have had a relatively plesiotypic aedeagus. At present, great diversity of aedeagal form precludes reconstruction of important features of the ancestral type.

If the slightly divided bifid ligula of specimens of *Agaricochæra* is hypothesized to have been derived independently from the similar state in members of the "*Sternotropa*" lineage, then *Agaricochæra* shares several apotypic conditions with members of the "*Gyrophæna*" lineage. Multiple origin of these character states in a number of well established lineages indicates that parallelism in these characters is common. At present, it seems most reasonable to assume that the bifid ligula is a uniquely derived character state within the gyrophaenines. Character states shared by members of *Agaricochæra* and the "*Gyrophæna*" lineage would then be parallelisms (Figure 259).

Among the genera of the "*Gyrophæna*" lineage, *Eumicrota* is hypothesized to be the sister group to *Phanerota* plus *Gyrophæna* (Figure 258). The hypothesis that the members of *Eumicrota* form a monophyletic group is supported by presence in all members of the genus of two unique apotypies. State 42 *D* is unknown in other gyrophaenines. Also, to my knowledge, it

Figure 257. Possible cladistic relationships of *Neobrachida* Cam.

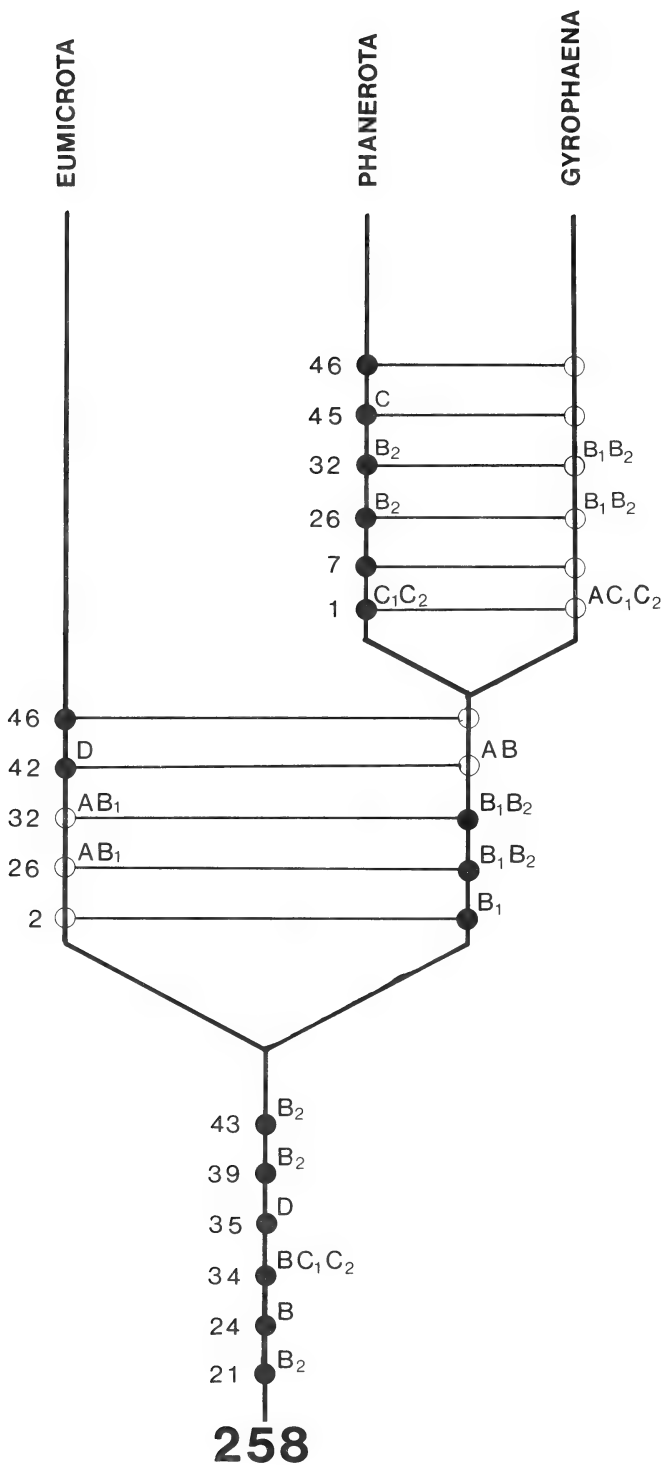


Figure 258. Hypothesized cladistic relationships among members of the “Gyrophaena” lineage.

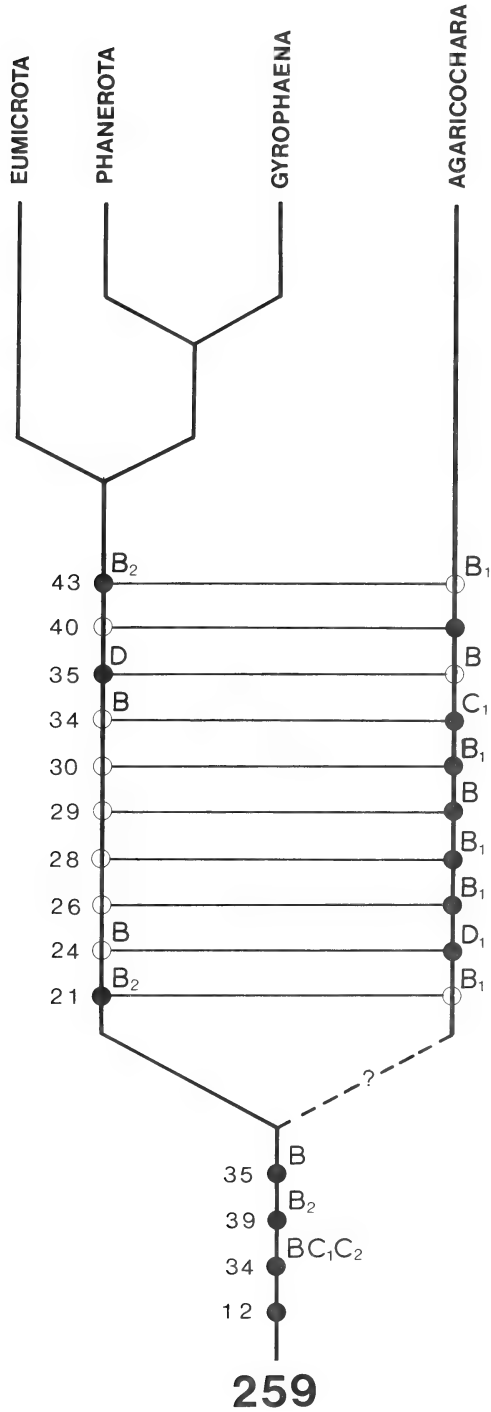


Figure 259. Hypothesized cladistic relationships of *Agaricochara* Kr., if hypothesized to be a member of the “Gyrophæna” lineage.

has not been reported among other aleocharines. In complete concordance with this character state is the fact that males of *Eumicrota* have a very distinctive aedeagal form, characterized by: a long, slender, often coiled flagellum; an elongate, slender apical process, often with a terminal knob or angulation; and a small basal bulb with a small, oval depressor plate placed far back on the proximo-ventral surface (Figure 197). This basic form is not obscured by interspecific variation.

The monophyly of the *Phanerota-Gyrophæna* lineage is weakly supported by three character states. Within this pair of genera, *Phanerota* is highly autapotypic in five characters, including a distinctive aedeagal form (Figures 195, 196), showing little variation among species (Character 46). There seems little doubt that *Phanerota* is a monophyletic assemblage.

There are no known uniquely derived character states shared by all members of the genus *Gyrophæna* to indicate that it is monophyletic relative to *Phanerota*. Therefore, at present, *Gyrophæna* must be considered paraphyletic in relation to *Phanerota*. This lack of unique apotypies may be a result of the extreme heterogeneity among the species now included in the genus. Diversity of body form within *Gyrophæna* is as great as the total range found among all other members of the Gyrophænina. Within *Gyrophæna* are found species whose members are markedly plesiotypic in most characters, to those which are markedly apotypic. Still, many monophyletic lineages can be recognized within *Gyrophæna*. Some of these may deserve generic status. However, revision of the generic status of *Gyrophæna* will require a phylogenetic study of the world fauna. This is a task of monumental difficulty in a group as diverse and inadequately known as *Gyrophæna*.

I retain *Phanerota* as a distinct genus for two reasons, even though it makes *Gyrophæna* as presently defined paraphyletic. First, I believe that additional study of *Gyrophæna* will result in it being divided into several monophyletic genera, one of which will probably be the sister group to *Phanerota*. Secondly, retaining *Gyrophæna* as a paraphyletic group graphically illustrates the need for study of this group at the world level.

The cladistic relationships of *Encephalus* cannot be determined at this time. Members of *Encephalus* are highly autapotypic. They share with members of the "*Brachida*" lineage a markedly robust body form, long mesosternal process (36 B), broadly rounded ligula (24 C), and, apparently, similar habits (see Life History). However, they share with members of the "*Gyrophæna*" lineage a single medial seta on the labium (25 B<sub>1</sub>), structure of the maxilla (particularly, a single distinct row of setae on inner face of lacinia and four distinct rows of flattened setae on apex of galea), and glabrous body integuments (1 C<sub>2</sub>). In addition, the aedeagus, especially the median lobe, is very similar to that of members of the *Gyrophæna nana* species group of SeEVERS (1951), as are the secondary sexual characteristics of males. Which of these similarities are parallelisms cannot be presently ascertained.

As discussed in the description of *Encephalus*, the New Zealand species of this genus may not be closely related to the Holarctic species, and perhaps should be placed in a separate genus. The elongate, entire ligula, prosternum with a distinct transverse carina, and maxillary structure, suggest these may be members of the "*Gyrophæna*" lineage.

## EVOLUTIONARY TRENDS IN GYROPHAENINA

### Introduction and Methods

A wide variety of staphylinids visit fresh mushrooms, and are commonly collected there in great abundance and diversity. However, most mushroom visitors appear to be predaceous on other arthropods which occur there. Most, indeed, are attracted to a mushroom after it begins



to decay. Some of these staphylinids may be truly mycophagous, and others may feed on the fungus facultatively. However, except for members of the few groups mentioned below, this has not been conclusively shown.

Among those staphylinids commonly found on mushrooms, gyrophaenines are unusual in that both larvae and adults are exclusively mycophagous. Since most staphylinids are predaceous, obligate mycophagy is a relatively rare, and apparently highly derived, habit within this family. Because of lack of knowledge of habits of most staphylinids, it is not known how many times obligate mycophagy has been independently derived. However, at present, I know of only two lineages of staphylinids conclusively known to be obligate fungus feeders in both larval and adult stages. The first of these are members of the subfamily Oxyporinae. All of these are included in a single genus, *Oxyporus* Fabricius, of world-wide distribution. Members of this genus are large, colorful beetles as adults, and both larvae and adults burrow into and feed on the flesh and gill tissue of fleshy mushrooms (Campbell, 1969, and personal observations).

The other known lineage of mycophagous staphylinids is the Gyrophaenina. The members of this subtribe are additionally unusual among fungivorous insects in that they are adapted to feed exclusively on the spore producing layer (the hymenium) of fresh mushrooms. This is a very important aspect of the relationship of gyrophaenines to mushrooms. There are a great many insects which feed on the flesh of fresh mushrooms, but most of these feed by burrowing into the flesh of the gills, stem or cap. Populations of insects feeding within the flesh are often very large, and both intra- and interspecific competition must often be quite intense in this habitat. Adaptation to feed exclusively on the hymenium allows gyrophaenines to use a spatial and nutritional resource within the mushroom habitat not extensively used by other mushroom-inhabiting insects. Thus, gyrophaenines avoid many of the direct interspecific competitive interactions common within the mushroom habitat. Indirect competition with other mushroom inhabitants still occurs, since any of the activities of these other organisms which influences productivity of the hymenium in turn affects gyrophaenines (see Natural History for a more detailed discussion of this).

This characteristic feeding habit of gyrophaenines combined with the unique characteristics of mushrooms as habitats have apparently provided opportunities for extensive radiation within the lineage, resulting in a group of great world-wide diversity. However, the radiation of gyrophaenines has produced some oddly disjunct evolutionary patterns, particularly in distribution of gyrophaenines among various mushroom groups.

In this section, I examine, in a very general way, evolution of the more important structural features which allow gyrophaenines to use the mushroom habitat in this unusual way. Then, by considering some of the more obvious general patterns of distribution of gyrophaenines within mushroom groups, I form generalizations and hypotheses about how these relationships between gyrophaenines and fresh mushrooms may have evolved.

To keep perspective, it is important to remember that life history and habits, host relationships, and systematics of gyrophaenines are incompletely known. Any generalizations made in this section are considered provisional and may require modification with additional study. The intent here is to develop initial hypotheses which provide a framework for formulation of specific questions about the evolution of gyrophaenines.

The basic method for inferring evolutionary pathways of diversification has been discussed by Anderson (1979). Fundamental to this approach is the method of phylogenetic systematics (Hennig, 1965, 1966; Ross, 1974 and others), which allows hypotheses to be formed about

phylogenetic relationships without requiring assumptions about specific evolutionary processes. Each monophyletic lineage is therefore a "natural" group in that it has a unique history. Such a system of relationships provides a base for making hypotheses about evolutionary diversification in structural, functional, ecological and other characteristics.

Anderson (1979) outlined the steps in deciphering "pathways of evolutionary divergence". These need not be repeated in detail here. The basis is that monophyletic terminal taxa are arranged in increasingly more comprehensive monophyletic groups on the basis of shared uniquely derived characters (autapomorphies). Results are depicted on a cladogram. Then additional data (ecological, structural, behavioral, etc.) are overlaid on the cladistic relationships and hypotheses developed about the evolutionary processes involved in diversification of the group. This method is used here to develop hypotheses about evolution of mouthpart structure and diversification of gyrophaenines in major host groups of mushrooms.

Detailed discussion of the phylogenetic analysis of the genera of gyrophaenines is presented above. The most parsimonious hypothesis of these cladistic relationships presently available is summarized in Figure 260. Two genera, *Encephalus* Kirby and *Neobrachida* Cameron, are of uncertain placement and are not included in the cladogram.

Major features of this cladogram of importance in subsequent analysis include:

1. the hypothesis that members of the subtribe Bolitocharina (= Group Bolitocharae of Seevers, 1978) form the sister group to the Gyrophaenina;
2. members of the Gyrophaenina form a monophyletic lineage;
3. within Gyrophaenina, three major lineages can be recognized, arbitrarily and informally designated the "*Brachida*" lineage, the "*Sternotropa*" lineage and the "*Gyrophaena*" lineage.

## Mushrooms as Habitats

*Introduction.*— Since gyrophaenines are obligatory inhabitants of fresh mushrooms, an understanding of general features of the mushroom habitat and the insects which occupy such a habitat is essential to unravelling major features of the evolution of gyrophaenines.

Much of the information about insects associated with fungi and most generalizations about characteristics of the mushroom habitat are derived from investigations on fungicolous Coleoptera (e.g., Benick, 1952; Donisthorpe, 1935, 1939; Lawrence, 1973; Minch, 1952; Paviour-Smith, 1959, 1960a, 1965b, 1969; Rhefous, 1955; Scheerpeltz and Höfler, 1948; Weiss, 1920a, 1920b, 1920c; Weiss and West, 1920, 1921). Additional information is available from studies of fungicolous Diptera (Buxton, 1960), and from faunistic studies of individual lignicolous fungi. For example, insects associated with *Pitoporus betulinus* (Bull. ex Fr.) Karst. have been studied by Paviour-Smith (1960b), Pielou (1966), and Pielou and Verna (1968); *Fomes fomentarius* (Linn. ex Fr.) Kickx. by Matthewman and Pielou (1971) and Pielou and Matthewman (1966); and various woody bracket fungi by Graves (1960). Other natural history studies of individual mushroom-inhabiting insects such as those of *Bolitotherus cornutus* (Heatwole and Heatwole, 1968; Liles, 1956; Pace, 1967) and *Tetratoma fungorum* Fabricius (Paviour-Smith, 1964, 1965a) provide additional information.

Elton and Miller (1954) grouped the fungus habitat into their "General System" with other small decomposing habitats, which included dead and decaying wood, carrion, dung, animal and small human artifacts, and slime molds. Elton (1966) noted that fungi form concentrated habitats which are ephemeral and interspersed within major habitats. He divided the resources available in fungi into spores, living fungus tissue, hard bracket fungi, and soft decaying fungi.

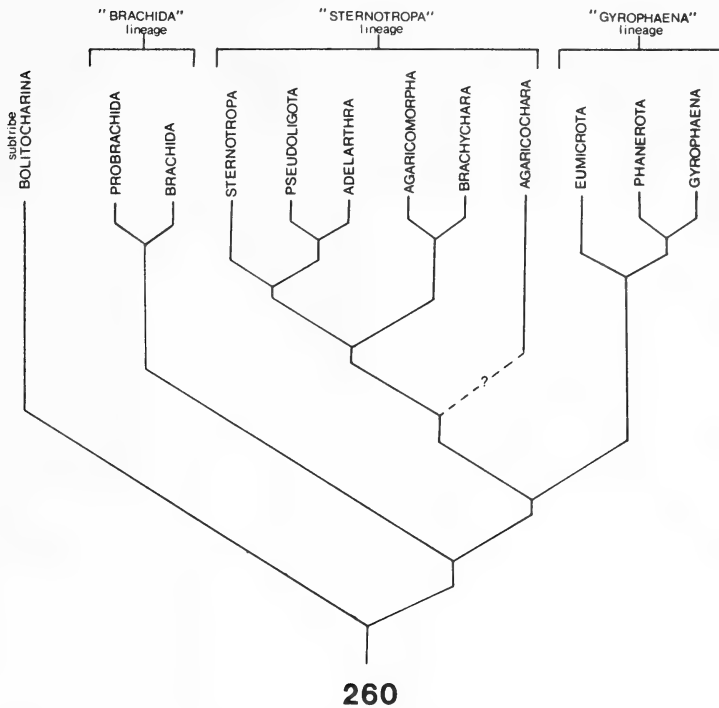


Figure 260. Summary of hypothesized cladistic relationships among genera of the Gyrophaenina.

He also pointed out that for analysis, whether the insects found on fungi were fungus feeders, wood borers, bark feeders, parasites, or accidental visitors, must be determined.

Scheerpeltz and Höfler (1948) recognized that, as habitats, fungi could be conveniently divided into hard forms on wood, soft forms on wood, and soft forms on the ground. They further divided soft fungi on the ground into five stages according to the state of development or decomposition. They suggested that as fungi pass through these successional stages, they alter as habitats for insects.

Paviour-Smith (1959, 1960a) extended and modified Scheerpeltz and Höfler's stages to include stages in growth and decomposition of lignicolous fungi. Additionally, she discussed the importance of the consistency of a fruiting body both when alive and upon decomposition and desiccation after death, as factors which may affect suitability as a breeding site for insects.

Hingley (1971), in studies of *Daldinia concentrica* (Bolt. ex Fr.) Ces. & Not., found that succession begins with a more host specific fauna and continues with more generalized fungus feeders and predators as the habitat characters of the mushroom change with age. In later stages, insects typically associated with fungi were replaced by those more typical of decaying wood.

Major fruitings of fungi may occur throughout the spring, summer or autumn, with particularly large fruitings after heavy rains in late summer and early autumn. After the fruiting body is fully developed, fertile spores from the hymenium are released. Following spore release, most soft fungi decay as a result of the action of bacteria and microfungi. Many polypores persist and produce additional releases of spores, often in response to wet weather.

The mode and rate of decomposition of mushrooms is dependent both on hardness ("woodiness") and location. Most ground fungi are in a humid microclimate and therefore deliquesce rapidly on decay. Rate of decomposition is dependent on a number of factors, including specific mushroom involved, temperature and humidity, and rainfall. Decay may be accelerated by burrowing and feeding activities of fungivorous Diptera and other arthropods. Also, exposure and trauma to inner tissues of the mushroom due to mechanical injury by slugs, birds or small mammals may speed decomposition. Most lignicolous fungi contain binding hyphae, and sometimes skeletal hyphae, and are therefore of tougher consistency than ground fungi. Most sporophores are also raised off the ground and are continually exposed to air currents. As a result, most fruiting bodies desiccate with age, and, upon death, become shrivelled or friable in texture. However, if such lignicolous fungi fall to the ground or become sodden, they decompose at a rate and in a mode similar to that of ground fungi.

Rate and mode of decomposition of different mushrooms are of importance to gyrophaenines, since they can inhabit only fresh mushrooms.

*General Characteristics of Mushrooms as Habitats.*— The mushroom habitat is actually a range of microhabitats dispersed within a more inclusive habitat, which have a number of similar characteristics to which any group of animals using them must respond. In general, mushrooms are:

1. ephemeral (many highly so)
2. unpredictable in time and space
3. extremely heterogeneous in physical and chemical characteristics.

It is difficult to think of another set of habitats having this particular combination of characteristics. In particular, extreme chemical and physical heterogeneity found among mushrooms makes them unusual as temporary habitats. Overlaid on these general characteristics are specific differences resulting from different rates and modes of decay, hardness, physical and chemical characteristics, seasonality, microdistribution, and abundance of members of individual mushroom species.

*Requirements for Use of the Mushroom Habitat.*— As discussed in relation to the life cycle of gyrophaenines above, many of the structural and natural history features of gyrophaenines are a response to unique features of the mushroom as a habitat. Exploitation of habitats with the general characteristics of mushrooms requires that gyrophaenines have unusual specializations. First, gyrophaenines must be able to determine when mushrooms are or are likely to be present in the general vicinity. This could present a problem, since gyrophaenines appear to become relatively inactive when mushrooms are rare. Inability to predict location and time of occurrence of individual mushrooms is important in this respect. While it may be possible for members of a gyrophaenine species to be adapted to become active when mushrooms are most likely to be present (e.g., after rains at certain times of the year) or restrict their activities to areas in which they are most likely to encounter mushrooms (certain microhabitats within a forest), it seems unlikely that they are able to adapt to predict location and time of occurrence of individual fruiting bodies or mushrooms of a particular species. For perspective, it is important to remember that for an animal the size of a gyrophaenine, distance between suitable mushrooms may be relatively very long even when mushrooms are common.

Associated with the general unpredictable characteristics of individual species or fruiting bodies is the requirement that gyrophaenines detect those mushrooms available for colonization, and distinguish suitable from unsuitable mushrooms quickly. It is important to emphasize that as far as is known, gyrophaenine adults must feed, mate and lay eggs on an

individual fruiting body and on this same plant larvae must mature before it decays.

The extreme chemical and physical heterogeneity of mushrooms is a very important constraint on gyrophaenines. Because of the general unpredictability of mushrooms, it would be ideal if members of a gyrophaenine species could use any mushroom encountered. However, it seems unlikely that members of any single gyrophaenine species could have the necessary range of physiological and structural adaptations which would allow efficient use of every mushroom encountered. Therefore, it seems more likely that only a very limited subset of available mushrooms are suitable for habitation by members on any particular gyrophaenine species. This substantially increases the difficulty for individual gyrophaenines in finding a suitable host.

Additionally, since numbers of individual mushroom species and diversity and species composition of the mushroom flora may vary seasonally, yearly or geographically, gyrophaenines must have some adaptive means of maintaining themselves whenever suitable fungi are not available.

Finally, of major importance is the physical and physiological ability to harvest the nutritional resources of the mushroom habitat while at the same time avoiding or overcoming competition with other organisms which are involved in similar activities.

### **Adaptations to the Mushroom Habitat**

*Morphological Adaptations.*— While association of gyrophaenines and fresh mushrooms is highly developed, gyrophaenines are not substantially different in body form and habitus from aleocharines with less specialized habits. The principal structural adaptations of gyrophaenines to mushrooms involve modifications of the mouthparts. In particular, the maxilla appears to be the main feeding structure, and is highly modified for feeding on the hymenium layer of fresh mushrooms. This may be the key structural adaptation of gyrophaenines, since it allows them to use the mushroom habitat in a very unusual way and subsequently affects other characteristics of the beetle-mushroom association.

Characteristics of the adult maxilla are illustrated in Figures 73, 235 and others. (Here I describe only the adult structure. The maxillae of larval gyrophaenines parallel those of adults in both structural and functional characteristics to a remarkable degree. This is discussed in more detail below.) The general features of the gyrophaenine maxilla illustrated by Figure 73 include the following:

1. Apex of the lacinia is truncate, with a well differentiated patch of small, densely arranged teeth or spines, which I refer to as the "spore brush".
2. Inner face of the lacinia lacks teeth or spines.
3. Setae on the inner face of the lacinia are in a single, well defined row.
4. Setae on the apex of the galea are in four well separated rows.

In addition, the galeal setae are modified to subspatulate or plate-like structures (Figure 235).

Gyrophaenines feed by "grazing" maturing spores, basidia, cystidea and hyphae from the hymenium layer. This is apparently primarily accomplished by scraping the hymenium surface with the spore brush. The galeal setae form a cap over the apex of the lacinial spore brush and may prevent loss of material removed from the hymenium.

The function of the mandibles in feeding is unclear. Gyrophaenine mandibles are not highly modified to eat fungus in relation to those of less specialized aleocharines. However, they may function to remove food from the spore brush, form it into a bolus, and/or grind food.

It is possible to arrange known maxillary forms of gyrophaenines and closely related bolitocharines into a transformation series, as shown in Figure 261. Transformation in a number of different character systems include:

1. Modification of the apex of the lacinia from more or less acute to obliquely truncate. Associated with this is modification of the teeth on the apex of the lacinia from a loosely organized patch, weakly differentiated from spines and setae on the internal face of the lacinia to a distinct, well organized patch of small, closely spaced teeth ( $A \rightarrow B$ );
2. Progressive loss of teeth from the inner face of the lacinia ( $A \rightarrow B \rightarrow C$ ).
3. Reduction in setae on inner face of lacinia to a single row ( $A \rightarrow B \rightarrow C \rightarrow D$ ).
4. Reduction in number of rows of setae on galea from numerous, closely spaced rows to four well separated rows ( $A \rightarrow B \rightarrow C$ ).
5. Modification of galeal setae from filiform to subspatulate or plate-like ( $A \rightarrow B \rightarrow C$ ).

These modifications probably reflect increasing reliance on hymenium scraping as a feeding mechanism. Associated with this seems to be progressive loss of manipulative and grasping functions of the face of the lacinia as reflected by loss of teeth and spines in this area.

By superimposing these maxillary modifications on a simplified phylogeny of gyrophaenines, it is possible to make a tentative hypothesis about how hymenium feeding may have arisen in the gyrophaenine lineages.

Figure 262 shows the distribution of maxillary forms among the major lineages of gyrophaenines. Members of the subtribe Bolitocharina have maxillae with many relatively generalized features for aleocharines as a whole. Maxillae of members of the subtribe are probably more similar to those present in the common ancestor of bolitocharines and gyrophaenines than any maxillary form found among the gyrophaenines. Though bolitocharines inhabit fresh mushrooms, structure of the maxilla seems to indicate that they are not as highly specialized for fungus feeding as are gyrophaenines. As noted above, the exact relationship of bolitocharines and fresh mushrooms is unknown.

By time of origin of the gyrophaenines, the lacinial spore brush was well differentiated but some scattered teeth remained on the inner face of the lacinia; setae were numerous and scattered on the inner face of the lacinia; and galeal setae were unmodified and in numerous rows. Maxillae with these features characterize some members of the "*Brachida*" lineage. In general, maxillae of members of this lineage are the most plesiotypic found among gyrophaenines. It is important to note that feeding habits of members of this lineage are unknown. The habitat of the large majority of species in this lineage has not been recorded. While some members are occasionally found on mushrooms on logs (Benick, 1952), they are more commonly collected from moldy leaf litter or rotting grass tufts (Lohse, 1974, and others). Possibly, members of this lineage do not have an obligatory association with fresh mushrooms. The less highly derived mouthparts of members of the "*Brachida*" lineage are consistent with this hypothesis. This presents the possibility that adaptations in the maxilla of gyrophaenines may have been developed in response to general fungus feeding and later were modified to feed specifically on the hymenium layer of fresh fruiting bodies.

By time of origin of the ancestor of the "*Sternotropa*" plus "*Gyrophaena*" lineage, all the highly derived character states of the maxilla of gyrophaenines had developed (except for retention of scattered setae on the inner lacinial face in some members of the "*Sternotropa*" lineage). Uniformity of derived states in mouthpart structure among members of these two lineages, particularly complete loss of teeth from the inner face of the lacinia, a well differentiated, dense spore brush on the apex of the lacinia, and reduction of galeal setae to four

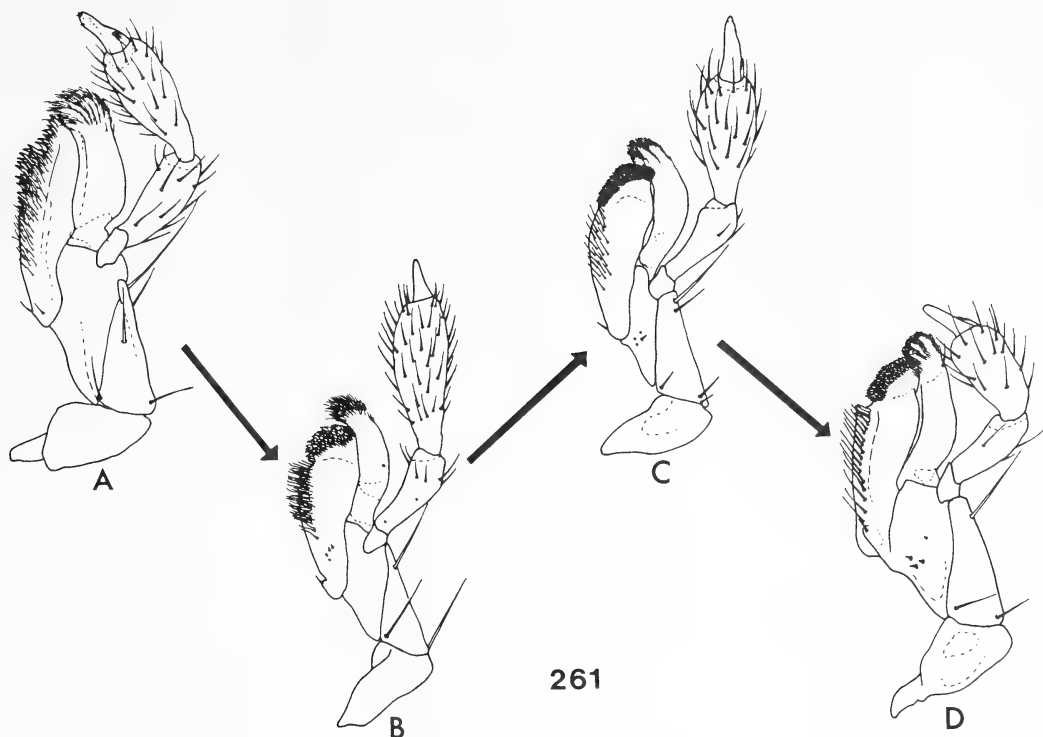


Figure 261. Transformation series in maxillary structure among members of subtribe Bolitocharina and Gyrophaenina. (*Neobrachida* and *Encephalus* not included.)

well separated rows of flattened setae, suggests that by time of origin of the ancestor of these lineages, gyrophaenines were fully committed to feeding on the hymenium of fresh mushrooms. This hypothesis is supported by the fact that all members of the “*Sternotropa*” and “*Gyrophaena*” lineages for which data are available are found in large numbers only in association with fungi, particularly fresh fruiting bodies.

It appears, therefore, that evolution of the characteristic way that gyrophaenines use the mushroom habitat is reflected in modifications in the maxilla. The early gyrophaenines may not have had an obligatory association with fresh mushrooms. Evolution of the ability to feed exclusively on the hymenium of mushrooms was apparently a later adaptation. This hypothesis is, of course, very sensitive to whether or not the major features of the proposed cladogram are correct. Falsification of aspects of the cladogram would require modification of these hypotheses.

Too little is yet known of structural variation in larval gyrophaenine mouthparts to allow a similar analysis of the evolution of these structures. However, the structural similarities between adult and larval maxillae strongly suggest that larvae of gyrophaenines are adapted to use the mushroom habitat in a way very similar to that of adults. Structural parallels in the maxillae of larval and adult gyrophaenines are remarkable (compare Figures 237 and 243). The spore brush on the apex of the mala of larval gyrophaenines is similar in all important respects to that found on the lacinia of adults. Additionally, it seems reasonable to hypothesize that the leaf-like scale at the outer apical angle of the mala of larvae may perform a function similar to that of the rows of subspatulate setae on the galea of adult gyrophaenines.

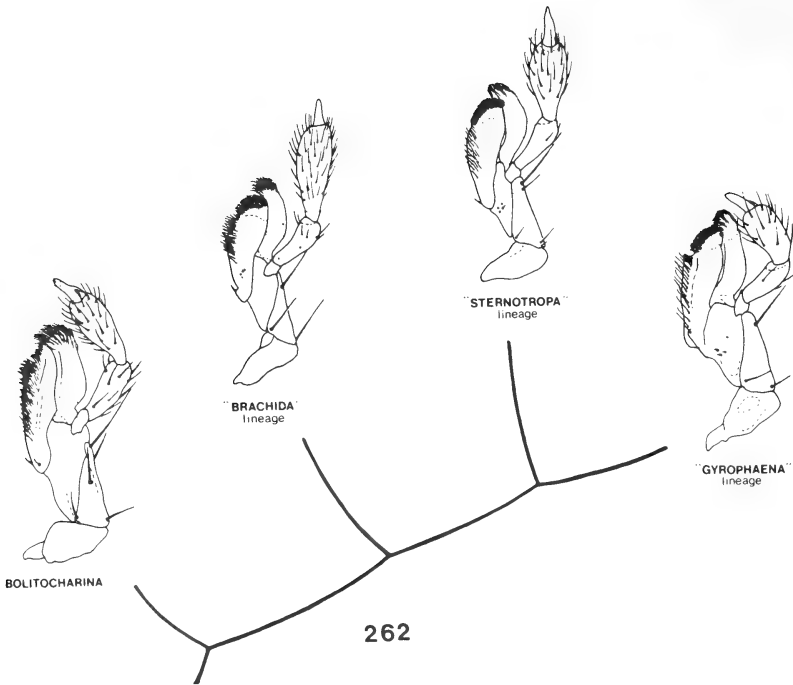


Figure 262. Maxillary forms among members of subtribes Bolitocharina and Gyrophaenina superimposed on a simplified cladogram.

Interestingly, habitat-related structural variations in adult maxillae discussed below are reflected in larval maxillae. This further suggests that larval maxillae are under a similar selective regime.

Several structural characteristics of gyrophaenines seem to be correlated with differing features of the various types of mushrooms occupied by them. Though these features appear to be correlated with various types of mushrooms, their origin is uncertain. Therefore, as discussed below, there are other possible explanations for these features than adaptation in response to selection.

Gyrophaenines associated with either persistent polypore or ephemeral gilled mushrooms tend to have a suite of external features which cause beetles most commonly found on mushrooms of either of these groups to have a similar habitus. It is important to emphasize that the correlation under discussion here is a tendency for gyrophaenines occurring in similar habitats to display similar external features. Exceptions are known, but the pattern of similarity is striking in spite of these. Members of those groups most commonly found on woody polypores tend to be, or have:

1. small size (the smallest gyrophaenines are in this group);
2. dark color, usually unicolorous piceous, black, brown or red-brown;
3. more or less sublimuloid body form or abdomen sides converging from base to apex;
4. body densely, uniformly covered with small microsetae;
5. macrosetae short, inconspicuous (but not in some *Sternotropa* and *Adelarthra*);
6. pronotum markedly transverse;



7. pronotum with hind borders markedly to moderately bisinuate;
8. pronotum lateral borders deflexed so that hypomera invisible in lateral aspect; and
9. apico-lateral angles of elytra markedly to moderately sinuate.

In contrast, members of those groups of gyrophaenines most commonly found on fleshy gilled mushrooms tend to be, or have:

1. larger size;
2. generally lighter color, often bicolorous, with both lighter and darker areas on same beetle;
3. more or less parallel-sided body;
4. microsetae on body fewer; head, prothorax and abdomen subglabrous;
5. macrosetae more prominent, larger;
6. pronotum less transverse;
7. pronotum with base slightly to not bisinuate;
8. pronotum lateral edges less deflexed so that hypomera moderately to broadly visible in lateral aspect; and
9. apico-lateral angles of elytra slightly to not sinuate.

Information about details and variation on these generalizations can be found by referring to the Structural Features section or the generic descriptions.

Whether cause and effect are involved in these correlations is not clear. Uniform structural features among members of a group may result from selection for similar characteristics by features of the habitat, similar phylogenetic ancestry, or both. Marked correlation of these external features with polypore or gilled mushroom habitats suggests that contrasting characteristics of the habitats may be selecting for these features. However, it has been argued above (see Character Analysis) that for each of the features correlated with polypore mushroom habitats, except size and color, the out-group comparisons within aleocharines suggest that they are best interpreted as ancestral (plesiotypic) within Gyrophaenina. Small size and dark color may be adaptations to features of the polypore habitat, but this is difficult to evaluate without additional data.

If these suppositions are correct, then those structural features correlated with gilled mushroom habitats are in some way selected for by the habitat. This hypothesis is further correlated by the relative phylogenetic position of the gyrophaenine groups which occur most commonly on gilled mushrooms (see Table 4). Additionally, within the heterogeneous assemblage of species presently included within *Gyrophaena*, different species are known which have external features typical of gyrophaenines from either polypore or gilled mushrooms. These seem to correlate well with the patterns of host preference described above. For example, members of *Gyrophaena hubbardi* SeEVERS and related species which are apparently most common on polypores, are difficult to separate on superficial external characters from members of the "Sternotropa" lineage.

Possibly, adaptations for life between gills of mushrooms in constant contact with the hymenium layer are involved in producing a tendency to have similar features in those gyrophaenines which live on gilled mushrooms. At present the data are much too tenuous and scattered to allow this set of correlated features to be evaluated further. Additional study is needed to determine if these patterns remain intact under detailed scrutiny and to determine detailed features of the various types of mushroom habitat.

A second interesting correlation of structure with polypore and gilled mushroom habitats involves details of the maxillary structure of adult gyrophaenines. Those gyrophaenines which live on woody polypores have a lacinial spore brush with relatively more numerous closely

spaced, shorter teeth (Figure 236) in comparison to those living on gilled mushrooms (Figure 234). The most closely spaced, numerous teeth in the spore brush known to me characterize adults of *Brachychara* species (Figures 94, 237). Members of *Brachychara*, as far as is known, live only on polypores.

It seems reasonable to hypothesize that these differences in number and density of the teeth in spore brushes of gyrophaenines are in some way related to the different problems for feeding presented by polypore and gilled mushrooms. Hardness of the mushroom, and size, shape or accessibility of spores and the hymenium layer are possible factors contributing to this structural difference.

An additional interesting correlation is the tendency for those gyrophaenines which occupy polypores to have V-shaped or chevron-shaped setal patches on tergum 10, while those which are most common on gilled mushrooms have more or less square setal patches (see sections on comparative morphology and phylogenetic analysis for details). It is particularly interesting that a chevron-shaped setal patch appears to have been evolved at least twice in the "*Sternotropa*" lineage. It is not possible to evaluate this correlation further at this time. However, it is possible that the setal patch on tergum 10 is involved in cleaning behavior. If so, it suggests that the problems of keeping the integument clean may be different in the two types of mushrooms.

All of the correlations between habitat type and structure of gyrophaenines require additional study outside the range of this investigation. They are reviewed here primarily to introduce the interested student to other areas of gyrophaenine evolution and natural history which could be profitably investigated.

*Life Cycle and Behavioral Adaptations.*— Life cycle and behavioral adaptations of gyrophaenines to the mushroom habitat are discussed in more detail above. However, it is important to emphasize here that many of the features of the life cycles and behavior of gyrophaenines are almost certainly a direct result of the nature of mushroom habitats. Rapid colonization of fruiting bodies is apparently an adaptation in response to the ephemeral nature of mushrooms. The possibility of active aggregation of gyrophaenines discussed above (see Natural History) may be an adaptation to a combination of unpredictability and ephemerality of mushrooms. If a suitable mushroom were discovered by a member of a gyrophaenine species, attracting other gyrophaenines of the same species to the mushroom might both increase the mating success of the original individual on the mushroom and provide more efficient and quicker use of available mushrooms. However, at present, because too little is known of aggregation in gyrophaenines and effects of intraspecific competition among gyrophaenines, it is difficult to evaluate scenarios which would allow aggregation to evolve.

Mating on mushrooms may also be related to their ephemeral nature, but it may also be an adaptation resulting from increased efficiency of mating when many gyrophaenine adults are present on a single fruiting body. The limited circumstantial evidence that the preoviposition period is short and oviposition occurs soon after colonization is consistent with what might be expected from requirements of an ephemeral habitat. A prediction might be that females mated on one mushroom would colonize another and oviposit without mating again, but this has not been investigated.

Very rapid larval development is almost certainly an adaptation to the ephemeral nature of mushrooms. Associated with this is rapid initiation of feeding and apparently more or less continuous feeding activities described for larvae of *Phanerota fasciata* (Ashe, 1981a).

It seems reasonable to expect that those gyrophaenines which live on more persistent polypore mushrooms may be under less stringent requirements for very rapid colonization of fruiting bodies and rapid life cycle. This would, therefore, suggest that life cycle and behavior of those gyrophaenines which live on polypores may differ in minor or significant ways from those which live on gilled mushrooms.

Presence of adult gyrophaenines in moist litter and under logs may be an adaptation to survive when few or only unsuitable mushrooms are available for colonization.

As discussed below, the general patterns of host relationships of gyrophaenines are also likely to be adaptations to characteristics of the mushroom habitat.

### Patterns of Host-Mushroom Relationships

*Introduction.*— As Seevers (1951) pointed out, the problem of host relationships is important. In particular, an understanding of gyrophaenine evolution appears impossible without consideration of the origin of both broad and detailed features of host relationship patterns. I have, therefore, within the limitations of this study, attempted to gather host information for gyrophaenines and apply it to problems relating to gyrophaenine evolution.

Very little has been published about host relationships of gyrophaenines, especially for the North American fauna. Host lists for European gyrophaenines include Benick (1952) [all known records for Palearctic Region], Donisthorpe (1935) [England] and Scheerpeltz and Höfler (1948) [Austria].

For North America, the literature about hosts of gyrophaenines is notable by its absence. Insect inhabitants of various woody bracket fungi have been relatively well studied by Matthewman and Pielou (1971), Graves (1960), Graves and Graves (1966), Paviour-Smith (1960a, b), Minch (1952) and Pielou (1966). However, none of these mentions finding any beetles of the subtribe Gyrophaenina. Relatively few papers have been written describing insects of gilled mushrooms. These include Moennick (1939, 1944), Chagnon (1935) and Weiss and West (1920, 1921). Of these, Weiss and West (1920) list one host for *Gyrophaena* (= *Eumicrota*) *corruscula* Erichson, and Moennick (1939, 1944) lists hosts for *Gyrophaena* (= *Phanerota*?) *fasciata* (Say) and *Gyrophaena flavicornis* Melsheimer. Ashe (1981a) has listed hosts for *Phanerota fasciata* (Say), and (1982) hosts for *P. dissimilis* (Erichson).

Few of those who have examined the hosts of gyrophaenines have attempted to discern a pattern in those host relationships. An exception is Scheerpeltz and Höfler (1948). Also, White (1977) has attempted a general treatment of which mushrooms are most likely to form acceptable hosts for gyrophaenines. However, much of the understanding of the way fungus beetle host relationship patterns develop is from studies of beetles of the family Ciidae which occur on woody polypores (Paviour-Smith, 1960a, b; Lawrence, 1973).

Except where otherwise noted, the host-mushroom data presented in this section were collected by me incidental to collecting for systematic research. A single collection is here considered to be all the specimens collected from a single mushroom or from a closely associated group of mushrooms of the same species on the same day. Biases inherent in data collected and handled in this way include:

1. Relative abundance of different mushroom species makes uniform sampling of all available mushrooms difficult.
2. Number of fruiting bodies sampled per collection affects average number of beetles per mushroom.
3. Groups or clusters of mushrooms tend to attract more attention than single mushrooms.

4. Pooling of data from a number of fruiting bodies of the same mushroom species, even if closely associated, can obscure potential differences in the beetle fauna due to differences in ages of fruiting bodies, competition or possibly other factors.
5. Host information gathered while collecting for systematic research gives only limited data about the mushrooms on which gyrophaenines do not occur.

However, in spite of such potential biases, these data include more than 700 individual collections with host data and reflect predictable trends of abundance and distribution of gyrophaenines among mushrooms. These data provide patterns for a first analysis of gyrophaenine host relationships. However, more sophisticated analysis of host relationships will require data collected in a more rigorous way.

Mushrooms were identified using a number of popular and semi-popular identification guides. These included Smith (1958), Hesler (1960), Kauffman (1971), Smith and Smith (1973), Smith, Smith and Weber (1979), and others. Confident identification of many mushrooms to species is difficult for the non-specialist. I have, therefore, consistently been conservative in my identifications of fungi. If specific determination is in question, I have been satisfied with a generic determination in which I have confidence. Whenever possible I have collected voucher specimens of host fungi so that many host records can be verified or identified more precisely.

Patterns of host relationships can be discussed at a number of taxonomic levels. Each one of these levels provides different insight into evolution of gyrophaenines. In this section, I consider host relationships at three taxonomic levels: 1) intergeneric patterns, 2) broad intrageneric trends with the large genus *Gyrophaena*, and 3) interspecific patterns.

*General Distribution of Gyrophaenines among Mushroom Groups.*— The distribution of gyrophaenines within available mushrooms is surprising. There are many groups of fungi which produce macroscopic fruiting bodies (commonly called "mushrooms") on which gyrophaenines are virtually never found. These include stinkhorns (Phallales), bird's-nest fungi (Nidulariales), puffballs and earthstars (Lycoperdales), coral mushrooms (Clavariaceae), jelly fungi (Heterobasidiomycetes) and cup fungi (Ascomycetes). Other mushroom groups on which gyrophaenines are rare and which are probably rarely or never included among the preferred hosts of gyrophaenines, include the bolete mushrooms (Boletaceae) and the tooth fungi (Hydnaceae).

Reasons for absence of gyrophaenines from some fungi (stinkhorns, puffballs, jelly fungi) appear to be related to the fact that the spore producing tissue is not generally available. Absence from others (coral fungi, ascomycetes) has no obvious reason.

When considered in the perspective of all possible mushroom groups, gyrophaenines are found on a very limited selection of mushrooms. They are common only on members of the Polyporaceae of the Aphyllophorales, the pored mushrooms, and several families of the Agaricales, the gilled mushrooms. These two general groups of mushrooms differ mainly in that the hymenium of members of the Polyporaceae is produced on the inside of pores, while that of the Agaricales is produced on the surface of lamellae or gills.

For gyrophaenines, polypores and gilled mushrooms differ in a number of potentially important general characteristics. Habitat differences of probable importance to gyrophaenines are summarized in Table 3, and discussed more fully with possible consequences in sections about Natural History and Adaptations to the Mushroom Habitat. It is important to note here that mushrooms of these two groups differ in persistence, place of spore production, and rate and length of time of spore production. These two extremes of habitat characteristics are joined

Table 3  
General Characteristics of Polypore and Gilled Mushrooms as Habitats for Gyrophaenines

	<i>Polypores</i>	<i>Gilled</i>
1) Persistence	relatively long lived	short to very short lived
2) Spore Production	inside tubes	on surface of "gills"
3) Length of Spore Production	often sporadically over a long period	numerous spores produced over a short period

by a range of more or less persistent gilled mushrooms and more or less ephemeral polypores. However, these contrasts suggest that, at least potentially, responses to the different conditions of these two major mushroom types could produce marked differences in life cycle, habits and population structure, and, subsequently, evolution of those gyrophaenines which occupy them.

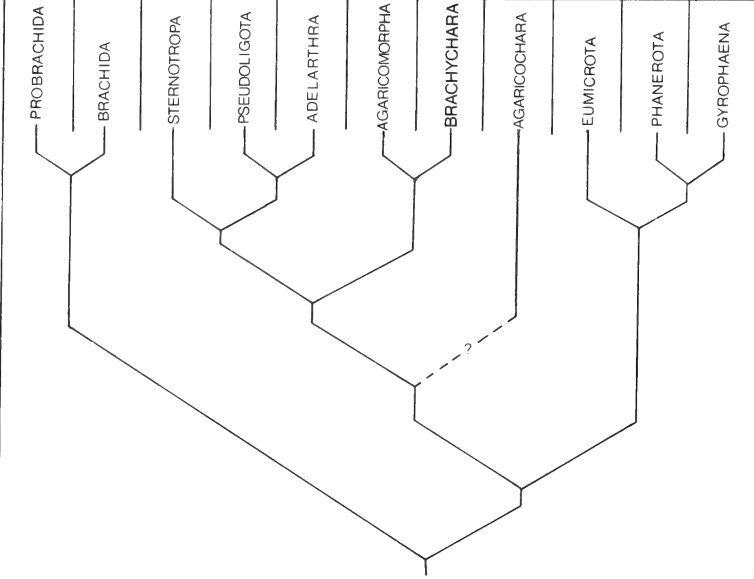
With these characteristics and possible consequences of the characteristics in mind, it is possible to examine patterns of distribution of gyrophaenines among mushrooms.

*Intergeneric Host Patterns.*— At the very broadest level of host relationships that has any information, it is possible to consider occurrence of genera among major habitat types of mushrooms, which are subjective categories suggested by the criteria of habitat characteristics discussed above.

Table 4 is a generalized summary of the distribution of members of gyrophaenine genera among major habitat types within the mushrooms. Mushroom data have been collected by me except that the information for *Agaricochara* is from Scheerpeltz and Höfler (1948), Benick (1952) and Donisthorpe (1935), and that for *Pseudoligota* from label data and published habitat data (Cameron, 1920b, 1939). This table predicts that members of *Sternotropa* occupy woody polypores, although no data are available. The number of crosses refers to the relative number of species in that genus which are most common or limited to mushrooms of a particular type.

Table 4 indicates that it is possible to recognize four broad host groups among mushrooms inhabited by gyrophaenines. Group I is made up of those gyrophaenines for which nothing is known of the host relationships. Primarily this includes the members of the "*Brachida*" lineage. As discussed above, it is possible that members of this lineage do not have an obligatory association with fresh mushrooms. Group II is made up of those gyrophaenines which are restricted to woody polypores. This includes all members of the "*Sternotropa*" lineage for which information is available, some members of *Eumicrota*, and a few *Gyrophaena*. Group III includes those which are most common on fleshy polypores. Gyrophaenines which occupy mushrooms of this type usually have host ranges which overlap into the persistent gilled mushrooms and woody polypores. Gyrophaenines which occupy Group III type habitats include most *Eumicrota* and some *Gyrophaena*. Group IV is made up of those gyrophaenines which are restricted to or most common on gilled mushrooms. This includes the most members of

TABLE 4  
Generalized distribution of members of gyrophaenine genera  
among major mushroom groups

UNKNOWN	++++	+++										
BOLETES									+-		+-	
GILLED MUSHROOMS									+-	+++	++++	
PERSISTENT GILLED MUSHROOMS <small>usually stemless on logs</small>									++	+++	++	
FLESHY POLYPORES		+				++			+++	+-	+	
WOODY POLYPORES		+	??	++++	?	++++	++++	++++	++		+	
RESUPINATE POLYPORES			?	?		+	+	+	+			
++++) very abundant												
+++)												
++)												
+) rare												
+ -) occasional												

*Gyrophaena* and *Phanerota*.

It is obvious that most genera of gyrophaenines occupy polypores. However, it is possible that this is a taxonomic artifact. In contrast, the gilled mushrooms have been invaded only by the lineage which leads to *Gyrophaena* and *Phanerota*. However, it is among the gyrophaenines which occupy gilled mushrooms that the great species diversity occurs, mostly in the genus *Gyrophaena*.

This distribution of gyrophaenines among broad mushroom groups along with evolution of structural adaptations in feeding structures discussed above suggests that as a first hypothesis about broad trends, it is possible to consider gyrophaenine evolution as attainment of a series of

TABLE 5

Generalized distribution of North American members of major species groups of *Gyrophaena* and *Phanerota* among members of commonly encountered gilled mushroom families

beetle taxon	mushroom taxon	white					pink	light brown	chocolate brown	grey black
		spore color	spore color	spore color	spore color	spore color	spore color	spore color	spore color	spore color
		AMANITACEAE	LEPIOTACEAE	HYGROPORACEAE	RUSSULACEAE	TRICHOLOMATACEAE	RHODOPHYLLACEAE	CORTINARIACEAE	AGARICACEAE	COPRINACEAE
<b><u>GYROPHAENA</u></b> (spp. grps.)										
NANA grp.								++++		
KEENI grp.		+				+		+++		
LAETULA grp.		+			+	++				
EGENA grp.					++++					
AFFINIS grp.		++				+++				
CONICIVENTRIS grp.		+				+++		+		
PULCHELLA grp.		+			+	+++		+		
BIHAMATA grp.		++				++		++		
<b><u>PHANEROTA</u></b> spp.		+			+++	++				
+++++) very abundant                      ++++) abundant +++) common                                  +) rare										

adaptive zones. Phylogenetic relationships suggest that the ancestor of the "*Sternotropa*" and "*Gyrophæna*" lineages probably lived on polypore mushrooms. This hypothesis is strengthened by the fact that gyrophaenines which prefer to occupy polypores are found in both lineages. In contrast, the phylogenetic position and great species diversity of those groups which live on gilled mushrooms suggests that it is possible to consider evolution of the ability to use the more ephemeral and unpredictable habitat of gilled mushrooms as the attainment of a new adaptive zone, which was followed by extensive radiation. However, hypotheses about whether attainment of the adaptive zone is clade- or grade-based (has occurred only once or by a number of lineages) must await more complete systematic studies of the heterogeneous assemblage of species now included in the genus *Gyrophæna*. This problem arises because presence of some species within *Gyrophæna* which occur on polypores suggests that gilled mushrooms may have been invaded several times during the evolution of this lineage.

*Intragenetic Level Host Patterns.*— One of the most interesting characteristics of host patterns of gyrophaenines is the major groups of mushrooms within generally acceptable mushroom types which they rarely or never occur on. Table 5 provides a subjective diagram of the general distribution of members of the major species groups of *Gyrophæna* and *Phanerota* which occur on members of commonly encountered gilled mushroom families. This is compiled from my own host records for North American gyrophaenines and may not generalize to other areas with a different gyrophaenine fauna. Lack of records of gyrophaenines from members of a mushroom group does not indicate that gyrophaenines have not been collected on these mushrooms. Instead, it indicates that only isolated adult specimens have been collected and there is no indication that gyrophaenines ever occur on these mushrooms in large numbers. Table 5 shows that gyrophaenines have a curiously disjunct distribution within the available mushrooms. There are major groups of mushrooms, the families Lepiotaceae, Hygoporaceae, Agaricaceae, and Coprinaceae, which produce fruiting bodies, but which are seldom inhabited by gyrophaenines. In addition, not apparent from Table 5, is the fact that often, even within a single genus of mushrooms, the same disjunct patterns of gyrophaenine distribution may be found. Some species attract large numbers of gyrophaenines while others have few or no gyrophaenines on them.

There is no correlation between known physical and chemical characteristics of mushrooms and this distribution. Gyrophaenines occur on a large number of mushroom species which are known to be toxic, for a variety of reasons, to humans, and fail to occur on others which are innocuous, or even desirable food for humans.

It is also apparent from Table 5 that members of a species group are usually most common on one or a few mushroom families rather than being distributed generally throughout available mushrooms.

While these general patterns of distribution of gyrophaenines within gilled mushrooms are quite baffling at present, it is obvious that gyrophaenines are establishing criteria for characteristics of an acceptable mushroom host in an unexpected way.

*Species Level Host Patterns.*— The simplicity of a subjective diagram of distribution of gyrophaenines within mushroom groups such as that presented in Table 5 is belied by the complexity of host data when the distribution of individual species among available mushrooms is considered.

Presentation of the many hundreds of available host records for gyrophaenines is not possible in this study. However, details of the host records are important. Patterns of relationships only become apparent after a very large number of host records have been



examined. Instead, in this section, I present some of the more important patterns of host data that are encountered and give a summary of the host records of gyrophaenine species which illustrate this pattern. Detailed host data are available from the author.

Pattern 1 — Adults may be found on a wide variety of often distantly related mushrooms.

This is a very common pattern. Almost always, whenever a large amount of host data is available for a species, the variety of mushrooms on which adults have been found represents many genera and usually several families of mushrooms. This is illustrated by the collection records for *Phanerota fasciata* (Say) (Table 6). In 61 individual collections with host data, adults of this species have been collected on members of 11 genera of mushrooms in 4 families. However, it is important to note that specimens of *P. fasciata* have not been found on all possible mushrooms, including all brown and dark-spored mushroom families and all polypores.

Pattern 2 — Although adults of most species of gyrophaenines occupy a variety of mushrooms, they are usually more common on members of one or a few mushroom genera.

Table 7 summarizes the distribution of adult individuals of *Gyrophaena nanoides* Seevers in 11 collections. While adults of this species have been found on members of nine genera of mushrooms, large numbers of individuals have been found only on *Cortinarius* species. The collection data for *P. fasciata* also illustrate Pattern 2 (Table 6). Specimens of *P. fasciata* are most commonly collected on members of *Russula* Grey and *Lactarius* (D.C.) ex Grey (family Russulaceae).

Pattern 3 — A very few species of gyrophaenines seem to have a well defined host range.

I have 13 collections of *Gyrophaena egea* Casey with host data. Of these, nine are from members of *Lactarius*, and four are from specimens of *Russula* (total number of specimens, 368). I have not encountered this beetle on any other mushroom, even though I have collected extensively in areas where it is common. *Russula* and *Lactarius* together form a distinctive family of gilled mushrooms, the Russulaceae. This suggests that mushrooms in these genera may have chemical or physical properties of importance to these beetles. Pattern 3 is very uncommon among gyrophaenines, and I know of no other gyrophaenine for which adequate host data are available that show it.

Pattern 4 — There are a few species of mushroom which always support an extremely large population of gyrophaenines representing a large number of species.

*Amanita verna* (Fr.) Quel. in the Blue Ridge Mountains of North Carolina seems to be such a mushroom. I have collected 751 adult individuals representing 13 species from a single fruiting body, and, in all, I have collected 17 gyrophaenine species from this mushroom species. *Hypholoma fasciculare* Quel. in Europe may exhibit a similar pattern of gyrophaenine habitation (see Benick, 1952; Scheerpeltz and Höfler, 1948; Donisthorpe, 1935; and other host lists of European gyrophaenines).

Pattern 5 — While one may consistently and predictably find members of a species of gyrophaenine on specimens of a particular group of mushrooms, and only occasional specimens on other mushrooms, one may sometimes find them in large numbers on a mushroom from which they have not been previously collected.

Table 8 summarizes collection data with host records from *Gyrophaena monticola* Seevers. Adults of this species have been commonly collected on mushrooms in three genera of the Cortinariaceae and one genus of Crepidotaceae. This suggests that they prefer light-brown spored mushrooms. However, in one instance they have been collected in large numbers on specimens of *Pleurotus* (Fr.) Quel., a light spored mushroom which occurs on logs. Pattern 5 is commonly encountered and causes much of the problem in interpretation of these host data patterns.

Table 6  
Summary of Host Records for *Phanerota fasciata* (Say)

Mushroom Taxon	Total No. Collections	Total Specimens Collected
<sup>1</sup> <i>Amanita</i> spp.	11	83
<i>Amanitopsis</i> sp.	1	50
<sup>2</sup> <i>Clitocybe illudens</i>	3	61
<i>Lactarius</i> spp.	12	394
<i>Russula</i> spp.	22	329
Others (6 genera) <sup>3</sup>	12	41

<sup>1</sup>Most specimens from 2 collections from *A. solitaria* (Bull. ex. Fr.) (55 specimens), and 1 collection from *A. verna* (Fr.) Quel. (24 specimens).

<sup>2</sup>Most specimens from 1 collection (52 specimens).

<sup>3</sup>*Armillaria* (2 coll.), *Boletus* (2 coll.), *Clitocybe* (2 coll.), *Entoloma* (1 coll.), *Lepiota* (1 coll.), *Pleurotus* (4 coll.).

Table 7  
Host Records for *Gyrophæna nanoides* Seev.

Mushroom Taxon	Number Collections	Total Specimens Collected
<i>Amanita verna</i>	1	5
<i>Amanita</i> sp.	1	3
<i>Clitocybe clavipes</i>	1	2
<i>Clitopilus</i> sp.	1	1
<i>Collybia confluens</i>	1	1
<i>Cortinarius</i> spp.	2	63
<i>Mycena</i> sp.	1	1
<i>Pleurotus</i> sp.	1	3
<i>Russula crustosa</i>	1	1
<i>Tricholoma</i> sp.	1	1

patterns.

Other data sets show additional patterns, but those indicated above seem to be most common and important. (See White [1977] for a more general treatment.) It is apparent from these examples that specific patterns of host relationships between gyrophænines and mushrooms are very complex.

*Principal Patterns and Origin of Host Relationships.*— Although the patterns of host data are complex, the fact that it is possible to recognize any pattern at all indicates that

Table 8  
Summary of Host Records for *Gyrophaena monticola* Seev.

Mushroom Taxon	Number Collections	Total Specimens Collected
<i>Cortinarius</i> spp.	11	336
<i>Crepidotus</i> spp.	4	124
<i>Gymnopilus</i> spp.	3	83
<i>Pholiota squarrosa</i>	2	113
<i>Pleurotus ostreatus</i>	1	137
all other mushrooms (5 genera)*	5	35

\**Clitocybe* (1 coll.); Undet. Cortinariaceae (2 Coll.); Undet. Tricholomataceae (2 Coll.).

gyrophaenines distinguish between mushroom groups at some level. Though many of these patterns cannot be explained at present, a few generalizations can be made about characteristics of relationships between gyrophaenines and mushrooms. First, all species have a host range — no monophagous species are known. Secondly, host preferences (rather than obligatory relationships) are the rule. When “preferred” mushrooms are not available, “less preferred” mushrooms are used. Finally, adults may live and feed on mushrooms on which they cannot breed. This was originally suggested by Scheerpeltz and Höfler (1948). Circumstantial evidence (personal observations) continues to support this hypothesis, but it has not been carefully tested. Paviour-Smith (1960a) proposed that members of the beetle family Ciidae which live in woody polypores have a similar relationship to mushrooms. She proposed the term “headquarters” for the most preferred or commonest breeding mushrooms for the species of ciids in an area.

Probably, all of these general characteristics are responses to the nature of the mushrooms as habitats. In addition, the mushroom flora may vary tremendously in the course of a season. At times mushrooms are incredibly abundant in great taxonomic diversity. At other times in the season, there are few fruiting bodies or species available. Species composition of the mushroom flora also changes throughout the year. To use this habitat efficiently, gyrophaenines must be able to respond to this variability. Ideally, the ability to use all available mushrooms would be of greatest advantage to a gyrophaenine (Ashe, 1981a). This, however, does not appear to happen. The members of a gyrophaenine species apparently use only a limited part of the mushroom flora.

The distribution of gyrophaenines among mushrooms can be partially explained by the tentative hypothesis that members of a species have an evolved tolerance to a range of conditions presented by mushrooms. They will, therefore, tend to occur on any mushrooms which present these conditions (White 1977). Closely related mushrooms will tend to have similar physical and chemical characteristics. Consequently, the same gyrophaenine species are likely to occur on them. However, less closely related mushrooms may also have similar characteristics, at least as far as the characteristics of importance to the gyrophaenines are concerned. These less closely related mushrooms may therefore serve as a suitable host for members of a gyrophaenine species which is more commonly found elsewhere.

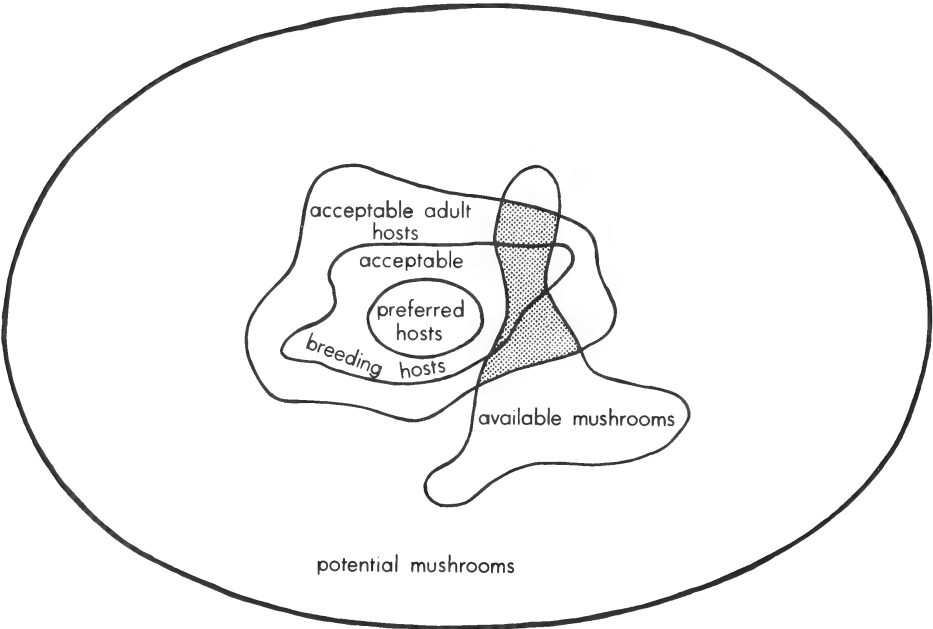
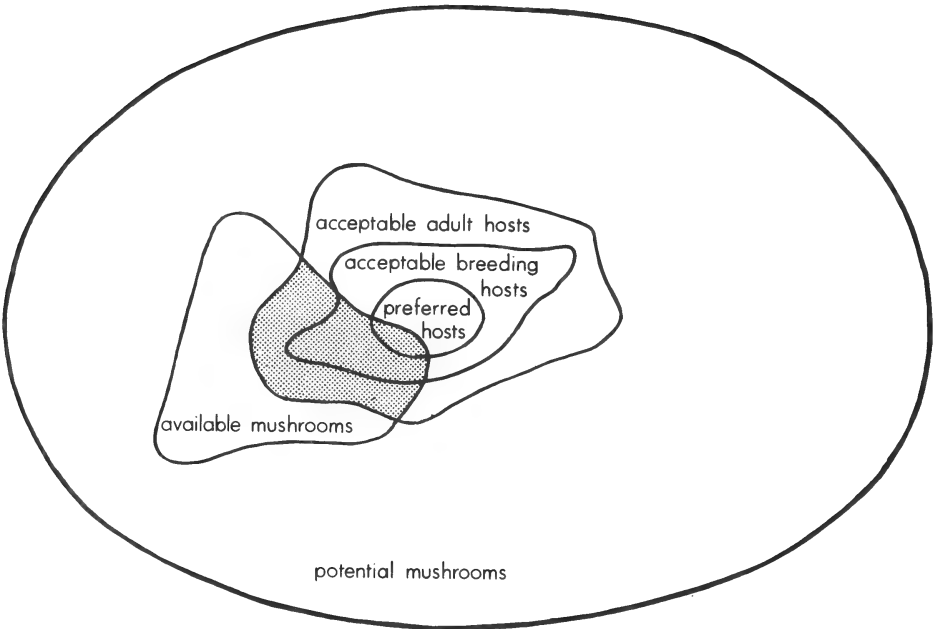


Figure 263. Schematic diagram illustrating how differences in available mushroom flora might overlap different parts of the "acceptability spectrum" of members of a gyrophaenine species.

Additionally, we should consider the working hypothesis that gyrophaenines distinguish between four broad categories of mushrooms: 1) "preferred hosts"; 2) "acceptable" breeding hosts; 3) "acceptable" adult hosts; and 4) unacceptable mushrooms. The boundaries between these broad categories are probably indistinct, and may vary depending on a variety of conditions. The distribution of available mushrooms would then overlap various portions of these acceptance categories for members of a gyrophaenine species. The way that this might occur is illustrated in the schematic diagram in Figure 263. The two diagrams in this figure show differences in the available mushroom flora which overlap different parts of the acceptability spectrum for all potential mushrooms for a species of gyrophaenine. Such differences in available mushrooms may result from seasonal, geographic or yearly variation.

If this generalization is correct, then several subsequent corollaries are suggested. First, examination of a limited amount of host data may present a confusing array of mushrooms. Patterns of the acceptability spectrum would become apparent only after examination of a large volume of host data. Second, this acceptability spectrum suggests that the preferred host need not be present for the members of a gyrophaenine species to survive. It implies that they are able to respond to variability in available mushrooms as discussed above.

In summary, it appears that at least two factors have had fundamental influence in evolution of the relationship between gyrophaenine staphylinid beetles and fresh mushrooms. First, evolution of a mouthpart structure that allowed the beetles to graze on the hymenium layer of the mushroom rather than feed directly on the fungal flesh opened a relatively unused portion of the mushroom habitat. Gyrophaenines thereby avoided much of the intense competition found among insects which feed on flesh of mushrooms.

Secondly, general characteristics of the mushroom as a habitat require that members of each species of gyrophaenine evolutionarily optimize among conflicting requirements. These include: need to use every mushroom encountered; physiological limitations suggested by the great chemical diversity of mushrooms; and physiological and competitive advantages expected from specialization.

Gyrophaenines seem to have resolved these conflicting requirements by evolving a tolerance to a range of physical and chemical characteristics provided by mushrooms. This tolerance range (reflected in the "acceptability spectrum" of a species) allows members of a gyrophaenine species to respond to seasonal, yearly, and geographic variation in the mushroom flora.

### **Adaptive Zones and Possible Evolutionary Scenarios**

*Evolutionary Scenarios.*— Eldredge (1979: 192) defines an evolutionary scenario as "a phylogenetic tree with an overlay of adaptational narrative". Scenarios are therefore inductive narratives designed to explain how some particular evolutionary pattern took place. However, he points out that most scenarios are not based on well corroborated phylogenetic trees. They are therefore mostly "fairy tales" based on untestable hypotheses about evolutionary processes or community organization, and do not represent "good science".

He suggests that there are at least two ways to improve scenarios: 1) base them more clearly on phylogenetic trees and 2) eliminate the more purely speculative evolutionary processes from them. If this is done the scenarios can be more informative than simple descriptions of where various groups occur. They become simplified models of major features of evolution of the group, and, as such, may stimulate further investigation. Also, when presented in this way, scenarios are both testable and refutable (Eldredge, 1979).

Scenarios are, however, far removed from the original data base from which relationships were hypothesized and numerous additional assumptions have been added. Therefore they may be expected to be wrong in detail. Strict adherents of "hypothetico-deductive" methods in science strongly disagree with *ad hoc* modification of scenarios as details are shown to be incorrect. However, modifications of scenarios to make them more consistent with new data would seem important, or alternately, as suggested by some cladists (Schaeffer, *et. al.*, 1972) scenarios should not be constructed at all. With respect to the possible heuristic value of scenarios this latter alternative seems the less desirable of the two.

Much of this confusion is lessened if it is realized that a scenario is not a single hypothesis. It is, instead, a series of hypotheses. It is rare that an entire scenario can be falsified at once. For this to be possible, a very basic assumption in the scenario must be shown to be false. More commonly, one or more less comprehensive assumptions within the scenario are falsified along with the subsequent hypotheses or parts of the scenario dependent on these assumptions. Modification of incorrect assumptions and hypotheses is what leads to the accusation that one is "fixing up" the scenario by *ad hoc* hypotheses. However, it appears that hypotheses in a scenario can be tested as long as the assumptions on which they are based are clearly stated.

An evolutionary scenario can be falsified by at least the following tests:

1. Since an evolutionary scenario is based on a cladogram, the scenario can be falsified by re-evaluation of sister group relationships.
2. Evolutionary scenarios (or specific hypotheses within the scenario) can be falsified by evidence that the ecological or habitat conditions postulated did not exist.
3. An evolutionary scenario can be falsified by additional life history information which indicates that the animals do not behave or relate to the environment in the way postulated.
4. An evolutionary scenario can be falsified by additional distributional data (either habitat or geographic) which are not consistent with the assumptions of the scenario.
5. An evolutionary scenario can be falsified by discovery of fossils for which the distribution in time and space is not consistent with that postulated in the scenario.

Additional tests for specific hypotheses within a scenario may be possible.

*Adaptive Zones and Major Features of the Evolution of Gyrophaenines.*—As pointed out by Eldredge (1979), it is very important that evolutionary scenarios be based explicitly on phylogenetic trees (*sensu* Eldredge, 1979, and Eldredge and Cracraft, 1980). Eldredge and Cracraft (1980) have correctly emphasized that only trees depicting hypothesized patterns of ancestry and descent have any meaning beyond the cladogram level of analysis. Additionally, higher taxa do not show patterns of ancestry and descent in the same context that species do. Therefore, for higher taxa, there is no formal distinction between the cladogram and a phylogenetic tree. Therefore, the phylogenetic tree on which this scenario of gyrophaenine evolution is based is the same as with the cladogram of genera depicted in Figure 260.

Cladistic relationships among gyrophaenine genera (Figure 260) coupled with distribution of major lineages of gyrophaenines among mushrooms (Table 4) suggests that the concept of "adaptive zones" can be useful in understanding how the broad host trends of gyrophaenines may have developed.

The concept of "adaptive zones" (Simpson, 1953; Bock, 1965) implies that the environment can be considered a mosaic of subhabitats, regions or zones within which characteristic adaptive complexes are required for survival of the organisms occupying those zones. Under this concept, evolution is viewed as acquisition of a specific adaptive complex which makes a series of previously unoccupied habitats (new adaptive zone) available to a group of organisms.

Evolution of the adaptive complex is usually taken to occur by a series of adaptive steps by species occupying a "transition zone" of habitats with intermediate characteristics. Of particular importance is attainment by a group of organisms of a zone that they were previously unable to occupy, and their subsequent diversification within that zone.

Under these criteria the major habitat types provided by mushrooms can be considered to represent a series of adaptive zones for gyrophaenines. Mushrooms provide a range of habitats from relatively persistent woody polypores to very ephemeral fleshy gilled mushrooms. More or less fleshy ephemeral polypores and more or less persistent gilled mushrooms provide a transition zone between these two habitat types.

Limited data suggest the following scenario. Lack of precise knowledge of the habits of members of the subtribe Bolitocharina and members of the "*Brachida*" lineage makes speculation about early history of gyrophaenines very uncertain. However, it seems reasonable to expect that gyrophaenines descended from an ancestor which was in some way associated with fungi, either obligatorily or facultatively. This ancestor may have fed facultatively on fungus mycelium and spores in litter or on fungus-covered logs.

Increasing reliance on feeding on fruiting structures of mushrooms selected for the specialized spore brush on the lacinia of gyrophaenines. Members of these early gyrophaenine species were probably not yet totally obligate inhabitants of fresh mushrooms. Mouthpart structure suggests that some members of the "*Brachida*" lineage may have habits similar to this. This was probably the first adaptive zone occupied by gyrophaenines.

Increasing reliance on hymenium scraping as a feeding mode led to the second adaptive zone of gyrophaenines, obligatory association with fresh mushrooms. This adaptive zone appears to have been reached by the ancestor of the "*Sternotropa*" plus "*Gyrophaena*" lineage. Additionally, presence of all members of the "*Sternotropa*" lineage and some members of the "*Gyrophaena*" lineage on woody polypores suggests that at this stage the gyrophaenines were limited to woody polypores.

Life cycle adaptations which allowed use of more ephemeral gilled mushrooms were probably important in opening up the final adaptive zone to gyrophaenines, that of gilled fungi. This appears to have been reached only by members of the "*Gyrophaena*" lineage, particularly *Gyrophaena* and *Phanerota*.

This scenario of major evolutionary trends in gyrophaenines is highly speculative. I provide it here in the hope that it will stimulate additional research to test it. This scenario is particularly sensitive to modification of cladistic relationships among gyrophaenine genera, increased knowledge of the habits of gyrophaenines, particularly members of the "*Brachida*" lineage and members of the subtribe Bolitocharina, and additional knowledge of distribution of gyrophaenines among mushrooms.

## PROSPECTUS: FUTURE TRENDS IN RESEARCH WITHIN THE GYROPHAENINA

Study of evolution of relationships between gyrophaenines and fresh mushrooms provides unique insights into the effect of ephemeral, unpredictable and highly heterogeneous habitats on patterns of evolution within groups which occupy such habitats. At present, this study is in the embryonic stages. Additional study of almost all aspects of gyrophaenine systematics and natural history would be valuable. Particularly useful would be life history and habit information for representative gyrophaenines which live on both soft and woody polypore mushrooms, members of the "*Brachida*" lineage, members of *Encephalus*, and other closely

related aleocharines. It would be very valuable to compare habits and life history of members of other aleocharine groups which are associated with fungi or mushrooms with those of gyrophaenines, especially if hypotheses about the effect of specific habits and habitat can be formulated for comparison. Additional host relationship data would be very useful, particularly if data were gathered rigorously to allow one to distinguish between breeding and feeding hosts and casual visits of adults to mushrooms, and how seasonal, yearly and geographical variation in mushroom flora affects use patterns. Ecological and physiological studies are needed to determine how gyrophaenines find mushrooms, and how they distinguish suitable from unsuitable mushrooms. Nothing is presently known about population dynamics of gyrophaenines and how these affect evolutionary patterns and processes.

The gyrophaenine fauna of most geographical regions is virtually unknown. My experience with the gyrophaenine fauna of Mexico, Central America, and, to a lesser extent, of South America indicates that there are a very large number of undescribed species, and probably undescribed genera, in these areas. It seems likely that the faunas of Africa, Southeast Asia, China, Australia, New Zealand and similar areas are also incompletely described. The fauna of India is probably moderately well described due to the studies of Cameron (1939), but, since he did not provide figures of male genitalia, most of his species are impossible to recognize without reference to types. This is true of most described gyrophaenines. Detailed systematic studies with complete descriptions and illustrations of gyrophaenine faunas of most areas would provide a much needed comparative base.

The heterogeneous assemblage of species presently included in *Gyrophaena* requires study on a world-wide basis. This is a monumental task, but can perhaps be approached by progressive study of increasingly comprehensive monophyletic groups.

Phylogenetic studies are possible at all levels of analysis. Many phylogenetically useful character systems are available and additional study is likely to reveal others. Phylogenetic studies are especially useful if combined with studies of habits and distribution so that hypotheses about evolutionary patterns and processes can be formulated and tested.

The limits of genera described here will probably require modification as the world fauna becomes better known. Also, subsequent analysis of character states in other groups of aleocharines may affect the cladistic hypothesis developed here. This will subsequently affect the hypotheses about evolution of gyrophaenines.

#### ACKNOWLEDGMENTS

I extend my sincerest appreciation to the many people who contributed substantially to this study both directly and indirectly.

J.F. Cornell encouraged my initial interest in beetles. He introduced me to gyrophaenines, stimulated, advised and provided enthusiasm for my early studies of these beetles, and set me on the path which led ultimately to this study.

Many coleopterists provided encouragement, support, advice and loan of specimens when I was still an amateur. Notable among these were H.R. Burke, H. S. Dybas, L.H. Herman, Jr., J.H. Lawrence, A.F. Newton and R.L. Wenzel.

G.E. Ball acted as my supervisor during this study and provided encouragement, intellectual stimulation and financial support (from Natural Sciences and Engineering Research Council of Canada Grant A-1399).



A CANACOL grant provided funds for study of gyrophaenines in the Canadian National Collection.

D.A. Craig, J.S. Nelson and W.M. Samuel of the University of Alberta, and J.M. Campbell of the Biosystematics Research Institute in Ottawa, formed my examining committee. They read and criticized this manuscript and made many helpful suggestions.

Numerous individuals and institutions have loaned specimens used in this study and/or provided services and courtesies during my visits to institutions. I offer special thanks to P.M. Hammond, M. Bacchus and G. Tibby for the many courtesies extended to me during my visit to the British Museum (Natural History), and for loan of specimens. I thank J.M. Campbell and D.R. Whitehead for hosting my visits to the Canadian National Collection and United States National Museum, respectively. A.F. Newton loaned me an excellent collection of gyrophaenines from Central America and Mexico from the collection of the Museum of Comparative Zoology. This collection provided essential information about intrageneric variation in New World gyrophaenines. J.F. Cornell, J.H. Frank, H.E. Frania and I.M. Moore loaned or donated specimens from their personal collections.

I thank the technical staff of the Entomology Department of the University of Alberta, particularly G.D. Braybrook, M.G. MacIntyre, and J.S. Scott, for a wide variety of services, advice and helpful suggestions during this study.

I am especially indebted to the many colleagues and fellow graduate students who have offered discussion, intellectual stimulation, encouragement and friendship during my years as a graduate student at the University of Alberta. For a variety of special contributions I especially thank R.B. Aiken, A. Borkent, J.M. Cumming, G.A.P. Gibson, J.D. Lafontaine, J.E. O'Hara, R.E. Roughly and K.A. Shaw.

I extend very special thanks to E.L. Maw who, in addition to friendship over the years, typed the draft of this manuscript in Textform, helped with editing and preparation of the published draft and offered many helpful suggestions. Without his help, production of this publication would have been a much more arduous experience.

This publication is slightly modified from a thesis presented to the University of Alberta, Edmonton, Alberta, in partial fulfillment of requirements for the degree of Doctor of Philosophy in Entomology. Portions of the "Evolutionary Trends" section and redrawn and slightly modified versions of Figures 260 to 263 and Tables 3 to 8 have been published in: O. Wheeler and M. Blackwell, editors, 1983. *Fungus/Insect Relationships. Perspectives in Ecology and Evolution*. Columbia University Press, New York. (in press).

Publication of this paper was supported by NSERC Grant A-1399 held by Dr. G.E. Ball. A grant from the Field Museum of Natural History provided for purchase of reprints.

#### LITERATURE CITED

- Anderson, N.M. 1979. Phylogenetic inference as applied to the study of evolutionary diversification of semi-aquatic bugs (Hemiptera: Gerromorpha). *Systematic Zoology* 28(4):554-578
- Arnett, R.H. 1968. *The Beetles of the United States (A Manual for Identification)*. American Entomological Institute, Ann Arbor, Mich., 1112 pp.
- Ashe, J.S. 1981a. Studies of the life history and habits of *Phanerota fasciata* (Say) (Coleoptera: Staphylinidae: Aleocharinae) with notes on the mushroom as a habitat and descriptions of the immature stages. *Coleopterists Bulletin* 35(1):83-96

- Ashe, J.S. 1981b. Pupal cell construction in the Aleocharinae (Staphylinidae). *Ibid.*, 35(3):341-343
- Ashe, J.S. 1982. Evidence on the species status of *Phanerota fasciata* (Say) and *Phanerota dissimilis* (Erichson) (Staphylinidae: Aleocharinae) from host mushroom relationships. *Ibid.*, 36(2):155-161
- Ashlock, P.D. 1974. The use of cladistics. *Annual Review of Ecology and Systematics* 5:81-99
- Ball, G.E. 1975. Pericaline Lebiini: Notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). *Questiones Entomologicae* 11:143-242
- Batten, R. 1973. Het voorkomen van *Gyrophaena*-soorten (Col.: Staphylinidae) op Walcheren. *Entomologische Berichten* 33:61-65
- Benick, L. 1952. Pilzkäfer und Käferpilze. Ökologische und statistische Untersuchungen. *Acta Zoologica Fennica* 70:1-250
- Bernhauer, M. 1916. Neue Staphyliniden des indo-malayischen Faunengebietes, besonders der Philippinen. *Verhandlungen der kaiserlich-königlich zoologisch-botanischen Gesellschaft in Wien* 66:418-431
- Bernhauer, M. 1922. Neue Staphyliniden aus Südamerika (23. Beitrag). *Verhandlungen der kaiserlich-königlich zoologisch-botanischen Gesellschaft in Wien* 71:1-23
- Bernhauer, M., and Scheerpeltz, Otto. 1926. *Coleopterorum catalogus. Pars 82, Staphylinidae* 6:499-988
- Blackwelder, R.E. 1936. Morphology of the coleopterous family Staphylinidae. *Smithsonian Miscellaneous Collections* 94:1-102
- Blackwelder, R.E. 1943. Monograph of the West Indian beetles of the family Staphylinidae. *United States National Museum Bulletin* 182:1-658.
- Blackwelder, R.E. 1952. The generic names of the beetle family Staphylinidae, with an essay on genotypy. *Ibid.*, 200:1-483
- Blatchley, W.S. 1910. *An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana*. Nature Publ. Co., Indianapolis, Ind., 1385 pp.
- Bock, W.J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Systematic Zoology* 14:272-278
- Bock, W.J. 1968. Phylogenetic systematics. *Evolution* 22:646-648
- Bonde, N. 1977. Cladistic classification applied to vertebrates. pp. 741-804. In: M. Hecht, P.C. Goody, and B.M. Hecht (eds.). *Major Patterns in Vertebrate Evolution*. NATO Advanced Study Institute Series. Plenum Press, New York.
- Böving, A.G., and F.C. Craighead. 1930. An illustrated synopsis of the principle larval forms of the order Coleoptera. *Entomologica americana* 11:1-351, 125 pls.
- Brundin, L. 1940. Studien über die *Atheta*-Untergattung *Oreostiba* Gangl. *Entomologisk Tidskrift* 18:56-130, 18 pls.
- Brundin, L. 1942. Monographie der palaearktischen Arten der *Atheta*-Untergattung *Hygroecia* (Coleoptera: Staphylinidae). *Annales des Naturhistorischen Museums in Wien* 53(2):129-300.
- Brundin, L. 1943. Zur Kenntnis einiger in die *Atheta*-Untergattung *Metaxyia* Muls. und Rey gestellten Arten. *Acta Universitat Lundensis* (N.F.) 54:38 pp., 7 pls.
- Brundin, L. 1948. *Microdota*-Studien. *Entomologisk Tidskrift* 69:8-66, 13 pls., 1 fig.
- Brundin, L. 1952. *Acrotona*-Studien (Gattung *Atheta*). *Ibid.*, 3:93-145, 78 figs.
- Brundin, L. 1954. Die palaearktischen Arten der *Atheta*-Untergattung *Dimetrota* Muls. et

- Rey. Eine systematische Studie. *Arkiv för Zoologi* 5:369–434, 117 figs.
- Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Pondonominae and Aphroteniinae and the austral Heptagyinae. *Svenska Vetenskaps Akademien Handlingar* 11:1–472
- Brundin, L. 1972. Phylogenetics and biogeography. *Systematic Zoology* 21:69–79
- Buxton, P.A. 1960. British Diptera associated with fungi. *Entomologist's Monthly Magazine* 96:61–94
- Cameron, M. 1920a. New species of Staphylinidae from Ceylon, Part II. *Entomologist's Monthly Magazine* 56:49–53, 94–99
- Cameron, M. 1920b. New species of Staphylinidae from Singapore. Part III. *Transactions of the Entomological Society of London* (1920):212–284
- Cameron, M. 1922. Descriptions of new species of Staphylinidae from the West Indies. *Annals and Magazine of Natural History* (Series 9) 9:113–128, 633–652
- Cameron, M. 1934. The staphylinid Coleoptera of the New Hebrides. *Stylops* 3:20–24
- Cameron, M. 1939. *The fauna of British India, including Ceylon and Burma. Coleoptera: Staphylinidae*, 4, pt.1. 410 pp.
- Campbell, J.M. 1969. A revision of the New World Oxyporinae (Coleoptera: Staphylinidae). *Canadian Entomologist* 101(3):225–268
- Casey, T.L. 1906. Observations on the staphylinid groups Aleocharinae and Xantholinini, chiefly of America. *Transactions of the Academy of Sciences of Saint Louis* 16:125–434
- Casey, T.L. 1911. New American species of Aleocharinae and Myllaeninae. *Memoirs on the Coleoptera* 2:1–259
- Chagnon, G. 1935. A preliminary list of the Coleoptera found on *Polyporus betulinus*. *Canadian Entomologist* 67:278
- Cracraft, J. 1974. Phylogenetic models and classification. *Systematic Zoology* 23:71–90
- Cracraft, J. 1978. Science, philosophy and systematics. *Systematic Zoology* 27:213–215
- Darlington, P.J., Jr. 1970. A practical critique of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. *Systematic Zoology* 19:1–18
- De Jong, R. 1980. Some tools for evolutionary and phylogenetic studies. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 18:1–23
- Donisthorpe, H. 1935. The British fungicolous Coleoptera. *Entomologists' Monthly Magazine* 71:21–31
- Donisthorpe, H. 1939. *A preliminary list of the Coleoptera of Windsor Forest*. Nathaniel Lloyd & Co., London. 126 pp.
- Dybas, H.S. 1976. The larval characters of featherwing and limulodid beetles and their family relationships in the Staphylinoidea (Coleoptera: Ptiliidae and Limulodidae). *Fieldiana, Zoology* 70:29–78
- Eichelbaum, F. 1913. Verzeichniss der von mir in den Jahren 1903 und 1904 in Deutsch- und BritischOstafrika eingesammelten Staphylinidae. *Archiv für Naturgeschichte* 79A(3):114–168
- Eldredge, N. 1979. Cladism and common sense. pp. 164–198. In: J. Cracraft and N. Eldredge (eds.) *Phylogenetic Analysis and Paleontology*. Columbia University Press. New York.
- Eldredge, N., and J. Cracraft. 1980. *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press, New York. 349 pp.
- Elton, C.S. 1966. *The pattern of animal communities*. Methuen, London. 432 pp.
- Elton, C.S., and R.S. Miller. 1954. The ecological survey of animal communities with a

- practical system of classifying habitats by structural characters. *Journal of Ecology* 42:460–496
- Erichson, W.F. 1837. *Die Käfer der Mark Brandenburg*. Vol. 1, Abt. 1. Berlin. 384 pp.
- Erichson, W.F. 1839–1840. *Genera et species staphylinorum insectorum coleoptorum familiae* pt. 1 (1839) and pt. 2 (1840). Berlin. pp. 1–400, 401–954
- Fauvel, C.A.A. 1875. Catalogue systématique des Staphylinides de la faune Gallo-Rhénane avec l'addition synonymique des espè européennes, sibériennes, caucasiques et méditerranéennes et descriptions nouvelles. *Bulletin de la Société linnéenne de la Normandie*, Caen, Ser. II, v. 6:545–738
- Fenyés, A. 1918. Coleoptera. Family Staphylinidae, Subfamily Aleocharinae. *Genera Insectorum* 173A:1–110
- Fenyés, A. 1918–21. Subfam. Aleocharinae. *Genera Insectorum* 173. Pasadena. 453 pp.
- Fenyés, A. 1921. New genera and species of Aleocharinae with a polytomic synopsis of the tribes. *Bulletin of the Museum of Comparative Zoology* 65(2):17–36
- Fowler, W.W. 1888. *The Coleoptera of the British Islands*. 2. Ashford, Reeve. London. 444 pp.
- Gaffney, E.S. 1979. An introduction to the logic of phylogeny reconstruction. pp. 79–111. In: J. Cracraft and N. Eldredge (eds.) *Phylogenetic Analysis and Paleontology*, Columbia Univeristy Press. New York.
- Ganglbauer, L. 1895. *Die Käfer von Mitteleuropa*. 2. Vienna. 880 pp.
- Graves, R.C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. *Annals of the Entomological Society of America* 53:61–78
- Graves, R.C., and A.C. Graves. 1966. The insects and other inhabitants of woody shelf fungi of the Southern Blue Ridge Region of Western North Carolina. I. Introduction, description of the habitat and the host fungi. *Annals of the Entomological Society of America* 59:381–389
- Griffiths, G.C.D. 1974. On the foundations of biological systematics. *Acta biotheoretica* 23:85–131
- Haeger, E. 1853. Naturgeschichte der *Gyrophaena manea* Erichson (Familie der Staphylinea). *Sitzungsberichte der Akademie der Wissenschaften in Wien* 10:460–464
- Hammond, P. 1975. The phylogeny of a remarkable new genus and species of gymnusine staphylinid (Coleoptera) from the Auckland Islands. *Journal of Entomology (B)* 44(2):153–173, 26 figs.
- Heatwole, H., and A. Heatwole. 1968. Movements, host-fungus preferences, and longevity of *Bolitotherus cornutus* (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America* 61:18–23
- Hecht, M.K., and J.L. Edwards. 1976. The determination of parallel or monophyletic relationships: the proteid salamanders — a test case. *American Naturalist* 110:653–677
- Hecht, M.K., and J.L. Edwards. 1977. The methodology of phylogenetic inference above the species level. pp. 3–51. In: M.K. Hecht, P.C. Goody, and B.M. Hecht (eds.). *Major patterns in vertebrate evolution*. NATO Advanced Study Institute Series. Plenum Press. New York.
- Hennig, W. 1965. Phylogenetic Systematics. *Annual Review of Entomology* 10:97–116
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana. 263 pp.
- Herman, L.H. 1972. Revision of *Bledius* and related genera. Part I. The *Aequitorides*, *Mandibularis* and *Semiferrugineus* groups, and two new genera (Coleoptera; Staphylinidae, Oxytelinae). *Bulletin of the American Museum of Natural History* 149:1–254
- Hesler, L.R. 1960. *Mushrooms of the Great Smokies*. University of Tennessee Press.

- Knoxville. 289 pp.
- Hingley, M.R. 1971. The ascomycete fungus, *Daldinia concentrica*, as a habitat for animals. *Journal of Animal Ecology* 40(1):17–32
- Hoeg, N. 1945. Beitrag zur Systematik der Aleocharinen. Über die Behaarung des Thorax bei der Gattung *Atheta* Thomson. *Entomologische Meddelelser* 24:264–286
- Hull, D.L. 1970. Contemporary systematic philosophies. *Annual Review of Ecology and Systematics* 1:19–54
- Hull, D.L. 1974. *Philosophy of Biological Science*. Prentice-Hall. Englewood Cliffs, N.J. 148 pp.
- Hull, D.L. 1979. The limits of cladism. *Systematic Zoology* 28:416–440
- Inger, R.F. 1967. The development of frogs. *Evolution* 21:369–384
- Jacquelin du Val, C. 1857–1859. *Genera des Coléoptères d'Europe*. Vol. 2. Paris. 1–40
- Kauffman, C.H. 1971. *The gilled mushrooms (Agaricaceae) of the Michigan and the Great Lakes Region. I & II*. Dover Publications Inc. New York. 924 pp.
- Kirby, W. 1832. New genera and species. In: J.F. Stephens. *Illustrations of British Entomology, Mandibulata*. Vol. 5. London. 240 pp.
- Klimaszewski, J. 1979. A revision of the Gymnusiini and Deinopsini of the World (Coleoptera: Staphylinidae, Aleocharinae). *Agriculture Canada Monograph* No. 25, 169 pp.
- Kluge, A.G. and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18:1–32
- Kraatz, G. 1856. *Naturgeschichte der Insecten Deutschlands. Abt. 1, Coleoptera*. Vol. 2, pt. 1–2. Berlin. pp. 1–376
- Kraatz, G. 1858. *Ibid.*, pt. 5–6. Berlin. pp. 769–1080
- Kreiger, L.C. 1967. *The Mushroom Handbook*. Dover Publications Inc. New York. 560 pp.
- Lacordaire, J.F. 1854. *Histoire naturelle des insects. Genera des coléoptères*. Vol. 2. Paris. 548 pp.
- Lawrence, J.F. 1973. Host preference in ciid beetles (Coleoptera: Ciidae) inhabiting the fruiting bodies of Basidiomycetes in North America. *Bulletin of the Museum of Comparative Zoology* 145(3):163–212
- Lawrence, J.F., and A.F. Newton, Jr. 1980. Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). *Coleopterists Bulletin* 34:129–143
- Likovsky, Z. 1964. Beiträge zur Kenntnis der Tschechoslowakischen Arten der Gattung *Gyrophaena* Mannerheim (Col: Staphylinidae). *Acta Rerum naturalium Musei nationalis slovenici Bratislava*. 10:51–65
- Liles, M. 1956. A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). *Ohio Journal of Science* 56:329–337
- Lohse, G.A. 1974. *Die Käfer Mitteleuropas. Bd. 5. Staphylinidae II (Hypocyphtinae und Aleocharinae), Pselaphidae*. Goeke & Evers. Krefeld. pp. 1–381
- Mannerheim, C.G. 1830. Précis d'un nouvel arrangement de la famille des Brachélytres. *Memoirs of the Academy of Sciences of St. Petersburg* 1:413–501
- Matthewman, W.G., and D.P. Pielou. 1971. Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. *Canadian Entomologist* 103:775–847
- Mayr, E. 1974. Cladistic analysis or cladistic classification? *Zeitschrift für zoologische Systematik und Evolutionsforschung* 12:94–128
- Mayr, E. 1981. Biological classification: toward a synthesis of opposing methodologies. *Science*

214:510–516

- Minch, E.L. 1952. Insect inhabitants of *Polyporus betulinus*. *Journal of the New York Entomological Society* 60:31–35.
- Moennick, H. 1939. List of Coleoptera found living in and on various fungi. *Bulletin of the Brooklyn Entomological Society* 34:155–157
- Motschulsky, T.V. 1860. Énumération des nouvelles espèces de coléoptères rapportées de ses voyages. *Bulletin de la Société Impériale des Naturalistes de Moscou* 33: 539–588.
- Moore, I., E.F. Legner, and M.E. Badgley. 1975. Description of the developmental stages of the mite predator, *Oligota oviformis* Casey, with notes on the osmetarium and its glands (Coleoptera: Staphylinidae). *Psyche* 82:181–188
- Motschulsky, T.V. 1860. Énumération des nouvelles espèces de coléoptères rapportées de ses voyages. *Bulletin de la Société Impériale des Naturalistes de Moscou* 33: 539–588.
- Mulsant, M.E., and C. Rey. 1871–1875. *Histoire naturelle des coléoptères de France: Brévipennes (Aléochriens)*. Vol. 1 (1873), Vol. 2 (1874), Vol. 3 (1873), Vol. 4 (1875), Vol. 5 (1871)
- Mulsant, M.E., and C. Rey. 1872. Tribu des brévipennes: Famille des aléochariens: Huitième Branche: Bolitochares. *Annales de la Société linnéenne de Lyon* (Ser. 2) 19:91–413
- Nelson, G.J. 1972. Phylogenetic relationships and classification. *Systematic Zoology* 21:227–231
- Nelson, G.J. 1973. Classification as an expression of phylogenetic relationships. *Systematic Zoology* 22:87–91
- Nelson, G.J., and N.I. Platnick. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York. 567 pp.
- Pace, A.E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). *Occasional Papers of the Museum of Zoology, University of Michigan* No. 653, 15 pp.
- Palm, T. 1968. *Svensk Insectfauna, 9, Skalborggar. Coleoptera, Kortvingar: Fam. Staphylinidae. Unterfam. Aleocharinae* (Deinopsis — Trichomicra) (5). Stockholm. 112 pp.
- Paulian, R. 1941. Les premiers états des Staphylinoidea. *Mémoires du Muséum national d'Histoire naturelle* (NS) 15:1–361
- Paviour-Smith, K. 1959. *The ecology of the fauna associated with macrofungi growing on dead and decaying trees*. Unpublished thesis in Bureau of Animal Population Library, Oxford, England
- Paviour-Smith, K. 1960a. The fruiting bodies of macrofungi as habitats for beetles of the family Ciidae (Coleoptera). *Oikos* 11(1):43–71
- Paviour-Smith, K. 1960b. Insect succession in the “birch-bracket” fungus, *Polyporus betulinus*. *Proceedings of the International Congress of Entomology 1958* 1:792–796
- Paviour-Smith, K. 1964. Habits, headquarters and distribution of *Tetratoma fungorum* F. (Col.: Tetratomidae). *Entomologists' Monthly Magazine* 100:71–80
- Paviour-Smith, K. 1965a. Some factors affecting numbers of the fungus beetle *Tetratoma fungorum* F. *Journal of Animal Ecology* 34:700–724
- Paviour-Smith, K. 1965b. The life history of *Tetratoma fungorum* F. (Col., Tetratomidae) in relation to habitat requirements, with an account of eggs and larval stages. *Entomologists' monthly Magazine* 100:118–134
- Paviour-Smith, K. 1969. An attempt to correct some mistakes and misconceptions about fungus

- beetles and their habitats. *Entomologist* 102:86–96
- Peschke, K. 1978. Funktionsmorphologische Untersuchungen zur Kopulation von *Aleochara curtula* Goeze (Coleoptera, Staphylinidae). *Zoomorphologie* 89:157–184
- Pielou, D.P., and W.G. Matthewman. 1966. The fauna of *Fomes fomentarius* (Linn. ex Fries) Kickx. growing on dead birch in Gatineau Park, Quebec. *Ibid.*, 98:1302–1312
- Pielou, D.P., and W.G. Matthewman. 1966. The fauna of *Fomes formentarius* (Linn. ex Fries) Kickx. growing on dead birch in Gatineau Park, Quebec. *Ibid.*, 98:1302–1312
- Pielou, D.P., and A.N. Verna. 1968. The arthropod fauna associated with the birch bracket fungus, *Polyporus betulinus* in eastern Canada. *Ibid.*, 100:1179–1199
- Platnick, N.I. 1977. Cladograms, phylogenetic trees and hypothesis testing. *Systematic Zoology* 26:438–442
- Platnick, N.J. 1979. Philosophy and the transformation of cladistics. *Systematic Zoology* 28:537–546
- Platnick, N.J., and E. Gaffney. 1977. Systematics: a Popperian perspective. *Systematic Zoology* 26:360–365
- Platnick, N.J., and E. Gaffney. 1978. Evolutionary biology: a Popperian perspective. *Systematic Zoology* 27:137–141
- Rehfous, M. 1955. Contributions à l'étude des insectes des champignons. *Mitteilungen der schweizerische entomologische Gesellschaft* 28:1–106
- Reitter, E. 1909. *Fauna Germanica. Die Käfer des deutschen Reiches*. Vol. 2. Stuttgart. 220 pp.
- Rey, C. 1886. Larve de la *Gyrophaena affinis* Sahlb. *Annales de la Société linnéenne de Lyon* 33:163–165
- Ross, H.H. 1974. *Biological Systematics*. Addison-Wesley Co., Inc. Reading, Mass. 345 pp.
- Saether, O.A. 1979. Underlying synapomorphies and anagenetic analysis. *Zoologica scripta* 8:305–312
- Sawada, K. 1970. Aleocharinae (Staphylinidae, Coleoptera) of the IBP-station in the Shiga Heights, central Japan (I). *Bulletin of the National Sciences Museum* 13(1):21–64
- Sawada, K. 1972. Methodological research in the taxonomy of Aleocharinae. *Contributions of the Biological Laboratory of Kyoto University* 24(1):31–59
- Sawada, K. 1974. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). I. Amidobia. *Ibid.*, 24(3):145–186
- Sawada, K. 1977. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). III. Japanese species described by previous authors. *Ibid.*, 25(2):171–222, 22 figs.
- Schaeffer, B., M.K. Hecht, and N. Eldredge. 1972. Paleontology and phylogeny. *Evolutionary Biology* 6:31–46
- Scheerpeltz, O. 1930. *Käfer (Coleoptera). Tierwelt Mitteleuropas. Insecten* 2. 12:1–272
- Scheerpeltz, O. 1934. *Coleopterorum catalogus. Pars 130, Staphylinidae. VII. Supplementum II*. Berlin. pp. 1501–1881
- Scheerpeltz, O., and K. Höfler. 1948. *Käfer and Pilze*. Verlag für Jugend und Volk. Vienna. 351 pp., 9 pls.
- Schubert, K. 1908. Beitrag zur Staphylinidenfauna Ostindiens (West-Himalaya). *Deutsche entomologische Zeitschrift* 1908:603–625
- Seevers, C.H. 1951. A revision of the North American and European staphylinid beetles of the subtribe Gyrophaenae (Aleocharinae: Bolitocharini). *Fieldiana: Zoology* 32:659–762

- Seevers, C.H. 1957. A monograph on the termitophilous Staphylinidae (Coleoptera). *Ibid.*, 40:1–334
- Seevers, C.H. 1965. The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). *Ibid.*, 47:1–351
- Seevers, C.H. 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera, Staphylinidae). *Ibid.*, 71:1–289
- Sharp, D. 1876. Contributions to an insect fauna of the Amazon Valley: Coleoptera — Staphylinidae. *Transactions of the entomological Society of London* 1876:27–208
- Sharp, D. 1883–1887. *Biologia Centrali-Americana: Insecta, Coleoptera. 1. (pt. 2)*. London. pp. 145–312, pl. 6–7 (1883); pp. 313–392, pl. 8–9 (1884); pp. 393–536, pl. 10–13 (1885); pp. 537–672, pl. 14–16 (1886); pp. 673–824, pl. 17–19 (1887).
- Simpson, G.G. 1953. *The major features of evolution*. Columbia University Press. New York. 434 pp.
- Simpson, G.G. 1975. Recent advances in methods of phylogenetic inference. In: W.P. Luckett and F.S. Szalay (eds.). *Phylogeny of the Primates*. Plenum Press. New York. pp. 3–19
- Smith, A.H. 1958. *The Mushroom Hunters Guide*. University of Michigan Press. Ann Arbor. 197 pp.
- Smith, A.H., H.V. Smith and N.S. Weber. 1979. *How to know the gilled mushrooms*. Wm.C. Brown Co. Dubuque, Iowa. 334 pp.
- Smith, H.V., and A.H. Smith. 1973. *How to know the non-gilled fleshy fungi*. Wm.C. Brown Co. Dubuque, Iowa. 402 pp.
- Stephens, J.F. 1832. *Illustrations of British Entomology, Mandibulata*. Vol. 5. London. 240 pp.
- Thomson, C.G. 1860. *Skandinaviens Coleoptera*. Vol. 2. Lund. 304 pp.
- Thomson, C.G. 1867. Entomologiska anteckningen under en resa i Skåne 1866. *Öfversigt af kongl. Svenska Vetenskap Akademiens Förhandlingar* 24:39–52
- Topp, W. 1973. Über Entwicklung, Diapause und Larvalmorphologie der Staphyliniden *Aleochara morens* Gyll. und *Bolitochara lunulata* Payk. in Nordfinnland. *Annales Entomologici Fennici* 39:145–152
- Topp, W. 1975. Zur Larvalmorphologie der Athetae (Col., Staphylinidae). *Stuttgarter Beiträge zur Naturkunde, Ser. A (Biologie)* 268:1–23
- Watrous, L.E., and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30:1–11
- Weiss, H.B. 1920a. Coleoptera associated with *Polyporus versicolor* L. in New Jersey. *Psyche* 27:137–139
- Weiss, H.B. 1920b. The insect enemies of polyporid fungi. *The American Naturalist* 54:443–447
- Weiss, H.B. 1920c. Notes on the fungus beetle, *Cis vitula* Mann. *Psyche* 27:133–134
- Weiss, H.B., and E. West. 1920. Fungus insects and their hosts. *Proceedings of the Biological Society of Washington* 31:236–237
- Weiss, H.B., and E. West. 1921. Additional notes on fungus insects. *Ibid.*, 34:167–172
- Welch, R.C. 1964. *The biology of the genus Aleochara Grav. (Coleoptera, Staphylinidae)*. Unpublished thesis. University of London. 432 pp.
- Westwood, J.O. 1838. *An introduction to the modern classification of insects*. Vol. 2. London. pp. 1–48
- White, I.M. 1975. *Studies in the Aleocharine genus Gyrophaena Mannerheim (Coleoptera:*



- Staphylinidae). B.Sc. Thesis. University of London.
- White, I.M. 1977. The larvae of some British species of *Gyrophaena* Mannerheim (Coleoptera: Staphylinidae) with notes on the taxonomy and biology of the genus. *Zoological Journal of the Linnean Society of London* 60(4):283–318
- Whitehead, D.R. 1972. Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera. Carabidae: Scaritini). *Quaestiones Entomologicae* 8:131–348
- Wiley, E.O. 1975. Karl R. Popper, systematics, and classification: A reply to Walter Bock and other evolutionary taxonomists. *Systematic Zoology* 24:233–242
- Wiley, E.O. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, N.Y. 439 pp.
- Wilson, E.O. 1965. A consistency test for phylogenics based on contemporaneous species. *Systematic Zoology* 14:214
- Wüsthoff, W. 1937. Beitrag zur Kenntnis der europäischen Arten der Gattung *Gyrophaena*. *Decheniana* 95B:137–146, 12 pls.
- Yosii, R., and K. Sawada. 1976. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). II: Diagnostic characters of genera and subgenera with description of representative species. *Contribution of the Biological Laboratory of Kyoto University* 25(1):11–140, 59 figs.

INDEX TO NAMES OF INSECT TAXA AND HOST PLANTS  
(Synonyms in *italics*)

## FAMILY GROUP TAXA

Acarina, 231  
 Aleocharinae, 132, 140, 141, 155, 156,  
     238, 273, 275, 291  
 Aleocharini, 152, 155, 293  
 Athetini, 293  
 Bolitocharae, 161, 294  
 Bolitocharina, 153, 162, 239, 266, 294,  
     314, 318, 335  
 Bolitocharini, 152, 162, 238, 239, 292,  
     293, 294  
 Chironomidae, 141  
 Ciidae, 223, 323, 331  
 Coleoptera, 141, 314  
 Collembola, 231  
 Deinopsini, 141  
 Diptera, 314  
 Dorylomini, 159  
 Falagriini, 159, 293  
 Gymnusini, 141  
 Gyrophaenae, 236, 238, 244  
 Gyrophaenides, 236  
 Gyrophaenina, 132, 133, 140, 141, 142,  
     153, 156, 161, 222, 223, 236, 237, 238,  
     239, 240, 242, 244, 250, 253, 265, 266,  
     267, 272, 275, 276, 278, 279, 280, 292,  
     293, 294, 296, 305, 312, 313, 314, 321,  
     323, 346  
 Gyrophaenini, 236, 238  
 Habrocerinae, 276  
 Hoplandrini, 155  
 Myllaenini, 156  
 Nanosellinae, 231  
 Oligotini, 255  
 Oxypodini, 280  
 Oxyporinae, 313  
 Philotermitini, 292  
 Russulaceae, 329  
 Silusina, 155  
 Tachyporinae, 276  
 Trichophylinae, 276

## GENERA AND SUBGENERA

*Acanthophaena* Cameron, 146, 234, 244,  
     245, 246, 247, 248, 268  
*Adelarthra* Cameron, 142, 155, 156, 158,  
     161, 234, 239, 240, 258, 259, 260, 261,  
     276, 291, 302, 305, 307, 320  
*Agaricochara* Kraatz, 154, 155, 158, 161,  
     163, 164, 233, 234, 237, 238, 239, 241,  
     243, 244, 245, 246, 250, 255, 256, 264,  
     278, 291, 296, 302, 303, 308, 325  
*Agaricomorpha* new genus, 142, 145, 146,  
     154, 155, 156, 157, 158, 159, 160, 161,  
     162, 163, 233, 234, 237, 239, 241, 256,  
     262, 263, 264, 272, 291, 302, 305, 307,  
     308  
*Agaricophaena* Reitter, 244, 245, 246  
*Allocota* Bernhauer, 244, 245, 246  
*Allocota* Motschulsky, 246  
*Astilbus* Dillwyn, 246  
*Bolitochara* Mannerheim, 164, 246, 294  
*Brachida* Mulsant and Rey, 146, 151, 154,  
     156, 158, 159, 161, 163, 164, 222, 233,  
     234, 238, 239, 240, 252, 253, 254, 255,  
     262, 268, 270, 271, 272, 273, 274, 277,  
     291, 296, 299, 300, 307  
*Brachychara* Sharp, 132, 142, 143, 145,  
     150, 154, 155, 156, 158, 160, 161, 163,  
     234, 237, 238, 239, 241, 256, 261, 262,  
     263, 264, 276, 291, 302, 305, 307, 308,  
     322  
*Dacne* Latreille, 231  
*Diestota* Rey, 238  
*Encephalus* Kirby, 132, 142, 155, 156,  
     157, 159, 160, 161, 222, 234, 238, 239,  
     240, 241, 250, 251, 252, 274, 276, 291,  
     312, 335  
*Encephalus* Westwood, 238  
*Enkentrophaena* Eichelbaum, 245, 246  
*Eumicrota* Casey, 142, 146, 149, 154, 155,  
     156, 157, 158, 159, 161, 164, 233, 234,  
     237, 238, 239, 241, 244, 245, 249, 250,  
     274, 291, 308, 312, 325  
*Gymnusa* Graverhorst, 155, 162  
*Gyrophaena* Mannerheim, 132, 140, 143,

145, 146, 147, 148, 149, 152, 155, 156,  
157, 158, 159, 161, 163, 164, 222, 233,  
234, 237, 238, 239, 241, 242, 243, 244,  
245, 246, 247, 248, 249, 251, 252, 256,  
263, 274, 276, 291, 308, 312, 321, 324,  
325, 326, 328, 335, 336  
*Gyrophaena s. str.*, 244, 245, 250  
*Hoplomicra* Sharp, 238  
*Homalota* Mannerheim, 254  
*Hygropetra* Motschulsky, 238  
*Leptarthrophaena* Scheerpeltz and Höfler,  
148, 244, 245, 246  
*Leptusa* Kraatz, 294  
*Megalodacne* Crotch, 231  
*Neobrachida* Cameron, 155, 163, 234,  
239, 241, 259, 260, 274, 291, 302, 305,  
307, 314  
*Orphnebioidea* Schubert, 245, 246  
*Oxyporus* Fabricius, 231, 313  
*Phaenogyra* Mulsant and Rey, 145, 238,  
244, 245, 256  
*Phanerota* Casey, 142, 146, 149, 155, 156,  
157, 158, 159, 161, 163, 164, 233, 234,  
237, 238, 239, 241, 243, 244, 245, 246,  
247, 248, 256, 268, 274, 276, 291, 308,  
312, 326, 335  
*Phanerota s. str.*, 248, 249  
*Probrachida* new genus, 146, 147, 152,  
153, 154, 155, 156, 161, 163, 222, 234,  
239, 240, 252, 253, 254, 255, 270, 271,  
272, 273, 274, 277, 291, 296, 299, 300  
*Pseudoligota* Cameron, 142, 152, 154, 155,  
159, 161, 163, 234, 237, 239, 241, 258,  
259, 261, 291, 302, 305, 307, 325  
*Razia* Bernhauer, 246  
*Sternotropa* Cameron, 142, 143, 145, 154,  
155, 156, 157, 158, 159, 161, 163, 233,  
234, 239, 241, 255, 256, 257, 258, 259,  
260, 261, 264, 272, 274, 291, 302, 305,  
307, 325  
*Triplax* Herbst, 231  
*Tritoma* Fabricius, 231

## SPECIES AND SUBSPECIES

*abnormalis* (Bernhauer), *Allocota*, 246  
*affinis* (Sahlberg), *Leptarthrophaena*, 246  
*affinis* Cameron, *Pseudoligota*, 234  
*affinis* Sahlberg, *Gyrophaena*, 234, 243  
*africana* Bernhauer, *Brachida*, 234  
*americanus* Seevers, *Encephalus*, 149, 150,  
159, 234, 252  
*antennalis* Casey, *Gyrophaena*, 151, 234  
*apacheana* (Seevers), *Agaricomorpha*,  
147, 224, 234, 238, 263, 264  
*apacheana* Seevers, *Gyrophaena*, 256, 264  
*apicalis* Cameron, *Sternotropa*, 234  
*appendiculata* (Motschulsky),  
*Acanthophaena*, 246, 248  
*appendiculata* (Motschulsky), *Phanerota*,  
234  
*arrowi* Bernhauer, *Gyrophaena*, 143  
*aspera* Fauvel, *Agaricochara*, 234, 256  
*aterrima* Cameron, *Brachychara*, 234  
*atomaria* (Cameron), *Eumicrota*, 234  
*atomaria* Cameron, *Gyrophaena*, 234  
*barbari* Cameron, *Adelarthra*, 142, 143,  
145, 146, 157, 159, 222, 234, 260  
*batesi* (Sharp), *Probrachida*, 253  
*blackwelderi* Seevers, *Gyrophaena*, 234  
*boleti* (Linnaeus), *Agaricophaena*, 244,  
246  
*boleti* (Linnaeus), *Gyrophaena*, 234  
*brevicornis* Cameron, *Sternotropa*, 160,  
234  
*brevicornis* Sharp, *Brachychara*, 234  
*californica* Casey, *Gyrophaena*, 226, 234  
*carinata* (Sharp), *Probrachida*, 149, 234,  
253  
*carinata* Seevers, *Phanerota*, 234  
*castanea* Cameron, *Neobrachida*, 234, 259  
*championi* Cameron, *Gyrophaena*, 234  
*chippewa* Seevers, *Gyrophaena*, 234  
*compacta* Seevers, *Gyrophaena*, 142  
*complicans* Kirby, *Encephalus*, 222, 234,  
250, 252  
*coniciventrif* Casey, *Gyrophaena*, 163, 234  
*cornutus* (Panzer), *Bolitotherus*, 231, 314  
*corruscula* (Erichson), *Eumicrota*, 158,  
234, 245, 249

- corruscula Erichson, Gyrophaena, 323  
 crassa Sharp, Brachychara, 234, 261  
 cristophera Cameron, Gyrophaena, 243  
 curtula Goeze, Aleochara, 164, 225  
 densiventris Bernhauer, Brachida, 149, 150, 234  
 dissimilis (Erichson), Phanerota, 150, 151, 234, 248, 323  
 egena Casey, Gyrophaena, 146, 234, 329  
 elevata (Fauvel), Sternotropa, 234  
 elevata Fauvel, Brachida, 255  
 exigua Heer, Brachida, 146, 222, 234, 253, 255  
 fasciata (Say), Gyrophaena, 323  
 fasciata (Say), Phanerota, 142, 143, 224, 225, 226, 227, 234, 238, 246, 248, 322, 323, 329  
 flavicornis Cameron, Sternotropa, 234  
 flavicornis Melsheimer, Gyrophaena, 163, 323  
 frosti Seevers, Gyrophaena, 150, 234  
 fungorum Fabricius, Tetratoma, 314  
 fuscicollis (Seevers), Gyrophaena, 143, 163  
 geniculata (Sharp), Probrachida, 150, 234, 253  
 gentilis Erichson, Gyrophaena, 226, 228, 238, 243  
 gilvicollis Casey, Gyrophaena, 234  
 gracilis Seevers, Gyrophaena, 142, 145, 156, 234  
 hubbardi Seevers, Gyrophaena, 156, 234, 256, 276, 321  
 importuna Erichson, Brachida, 253  
 insigniventris (Cameron), Phanerota, 234  
 karyni Cameron, Pseudoligota, 234  
 laetulus Broun, Encephalus, 234, 251  
 laevicollis (Kraatz), Agaricochara, 161, 234, 238, 245, 255, 256  
 lamellata (Cameron), Phanerota, 234  
 longicornis Cameron, Sternotropa, 234  
 lunulata Paykull, Bolitochara, 153, 226  
 maculata Oliver, Diaperus, 231  
 manca Erichson, Gyrophaena, 243  
 minutissima Casey, Eumicrota, 234  
 modesta (Sharp), Probrachida, 149, 157, 234, 252, 253  
 modesta Say, Brachida, 253  
 moerens Gyllenhal, Aleochara, 226  
 monticola Seevers, Gyrophaena, 329  
 nana (Paykull), Gyrophaena, 144, 156, 227, 234, 242, 245, 252  
 nanoides Seevers, Gyrophaena, 234, 329  
 natalensis Bernhauer, Brachida, 234  
 nigra Cameron, Sternotropa, 234, 257  
 notha (Erichson), Brachida, 234, 253, 254  
 oviformis Casey, Oligota, 232  
 plicata (Fauvel), Enkentrophaena, 246  
 plicata (Fauvel), Gyrophaena, 234  
 pollens Sharp, Gyrophaena, 234  
 pulchella Casey, Gyrophaena, 142, 146, 163, 228  
 reyi (Sharp), Probrachida, 234, 253  
 robusta Cameron, Pseudoligota, 234  
 rosti (Schubert), Orphnebioidea, 246  
 rosti Schubert, Gyrophaena, 234  
 sculptipennis Casey, Gyrophaena, 144, 234  
 sexualis Bernhauer, Brachida, 253  
 simulans Casey, Gyrophaena, 228  
 socia (Erichson), Eumicrota, 158, 234  
 sparsa (Sharp), Probrachida, 149, 150, 234, 253  
 spatulata Seevers, Gyrophaena, 234  
 spinosa Seevers, Eumicrota, 234  
 strictula (Erichson), *Phaenogyra*, 245  
 strictula Erichson, Gyrophaena, 146, 234, 243  
 sublaevipennis Cameron, Brachida, 150, 151, 234  
 subnitens Casey, Gyrophaena, 234  
 timidula Erichson, Brachida, 253  
 tuberculiventris (Bernhauer), Gyrophaena, 234  
 varians (Sharp), Eumicrota, 234  
 varians Cameron, Pseudoligota, 151, 234, 258  
 varians Sharp, Gyrophaena, 250  
 vitrina Casey, Gyrophaena, 142, 143, 234  
 wisconsinica Seevers, Gyrophaena, 142  
 zealandica Bernhauer, Brachida, 255  
 zealandicus Cameron, Encephalus, 158, 161

234, 251

## HOST PLANTS

- Agaricaceae, 328  
Agaricales, 324  
*Amanita verna* (Fr.) Quel, 222, 329  
*Amanita verna* (Lam. ex Fr.), 132  
Aphyllphorales, 324  
Ascomycetes, 324  
Boletaceae, 324  
Clavariaceae, 324  
Coprinaceae, 328  
Cotinariaceae, 329  
Crepidotaceae, 329  
*Daldinia concentrica* (Bolt ex Fr.) Ces. &  
Not., 315  
*Fomes*, 224  
*Fomes fomentarius* (Linn. ex. Fr.) Kickx 314  
Heterobasidiomycetes, 324  
Hydnaceae, 324  
Hygoporaceae, 328  
*Hypholoma faciculare* Quel., 329  
Lepiotaceae, 328  
Lycoperdales, 324  
Nidulariales, 324  
Phallales, 324  
*Pitoporus betulinus* (Bull. ex. Fr.), 314  
*Pleurotus* (Fr.) Quel., 329  
Polyporaceae, 324  
Russulaceae, 329  
*Tricholmopsis rutilans* (Fr.) Sing., 226  
*Tricholoma*, 228  
*Tricholoma sulfureum* Fries, 228









# Quaestiones Entomologicae

A periodical record of entomological investigations,  
published at the Department of Entomology,  
University of Alberta, Edmonton, Canada.

Publication of *Questiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at The University of Alberta in Edmonton in 1922.

It is intended to provide prompt relatively low-cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the *Style Manual for Biological Journals*, published by the American Institute of Biological Sciences, Second Edition, 1964, except that titles of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required one in English, and one in another language, preferably in French.

Copy for illustrations must accompany the manuscript and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7.3 X 9 inches, or 19.7 X 13.2 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals: \$17.00 (Can.) to subscribers within Canada and \$17.00 (U. S.) for those outside Canada, per volume of four issues; single issues \$5.00. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions and exchanges should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

---

Published quarterly by:

Department of Entomology  
University of Alberta  
Edmonton, Alberta, CANADA  
T6G 2E3

---

**Second Class Mail Registration Number 5222**

Return Card/deliverable mail to the address above. Return Postage Guaranteed.

A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 20

Number 4

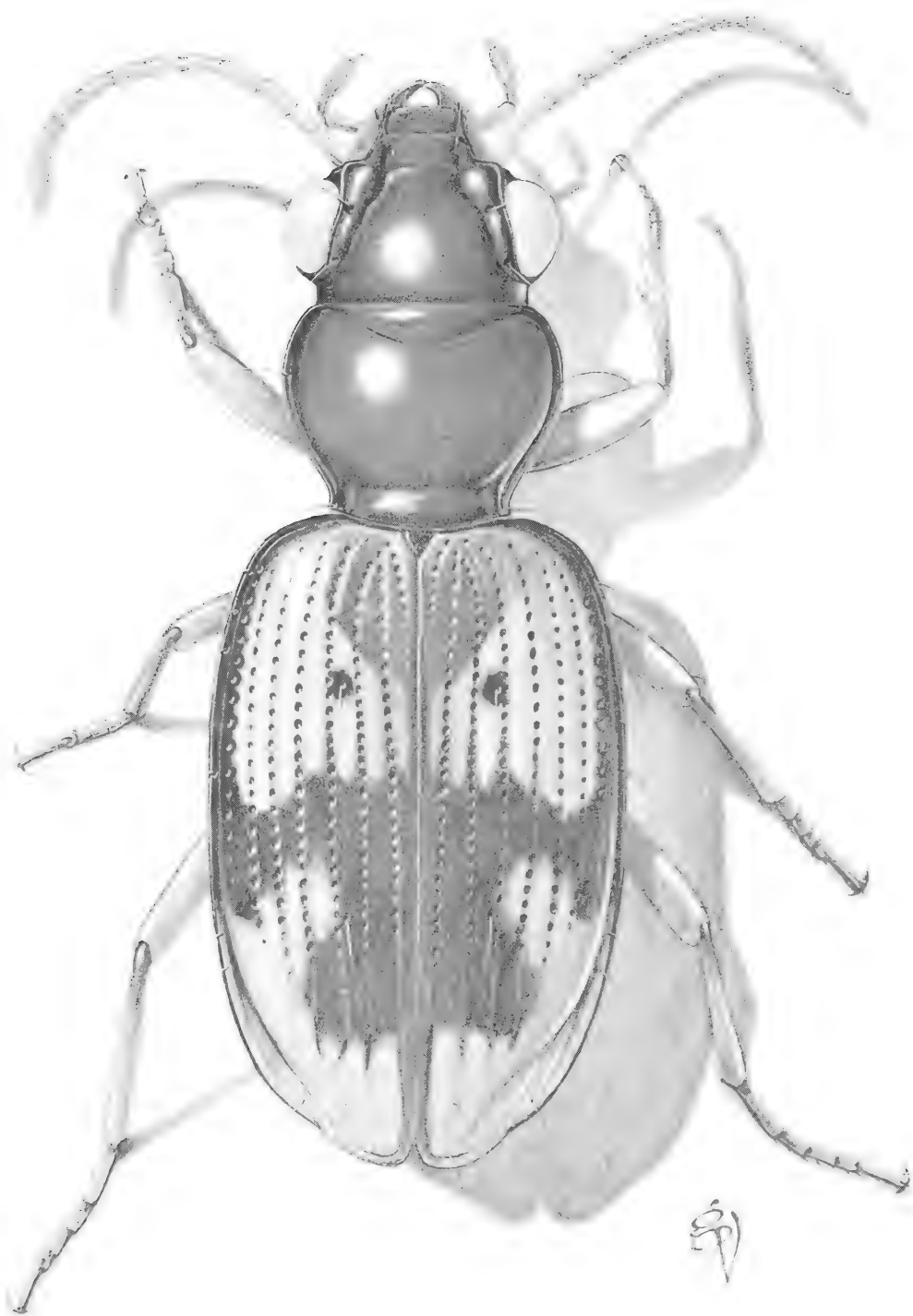
October 1984

## CONTENTS

Erwin and Sims—Carabid Beetles of the West Indies (Insecta: Coleoptera): A Synopsis of the Genera, and Checklists of the Tribes of Caraboidea, and of the West Indian Species .....	350
Book Review—Kryzhanovsky, O.L. 1983. Fauna of the U.S.S.R., new series no.128. Coleoptera. Volume 1, no. 2 .....	467
Editor's Acknowledgements .....	469
Index to Volume 20 .....	471







*Bembidion darlingtoni* Mutchler, dorsal aspect, male, from Soledad (Cienfuegos), Cuba.

**CARABID BEETLES OF THE WEST INDIES (INSECTS: COLEOPTERA): A SYNOPSIS  
OF THE GENERA AND CHECKLISTS OF TRIBES OF CARABOIDEA, AND OF THE  
WEST INDIAN SPECIES**

Terry L. Erwin  
and

Linda L. Sims

Department of Entomology  
Smithsonian Institution  
Washington, D.C. 20560  
U. S. A.

*Quaestiones Entomologicae*  
20: 351-466 1984

**ABSTRACT**

*The fauna of the Greater Antilles was extensively sampled and studied by P.J. Darlington, Jr., beginning with his early field trips there in 1934 and ending with his paper on tropical island carabids in 1970. The Lesser Antilles and Bahamas have had far less attention; most islands have not yet been sampled. The following tribes are recorded within the geographic area covered by the present study, which includes the Greater and Lesser Antilles, Bahamas, and most smaller islands not on the continental shelf: Carabini; Megacephalini; \*Cicindelini; Enceladini; Pseudomorphini; Scaritini; \*Clivinini; Ozaenini; Brachinini; \*Rhysodini; Trechini; Pogonini; \*Bembidiini; Morionini; \*Pterostichini; Panagaeini; Callistini; Oodini; Licinini; \*Harpalini; Ctenodactylini; Perigonini; Lachnophorini; Cyclosomini; Masoreini; Pentagoniini; Odacanthini; \*Lebiini; \*Zuphiini; Galeritini. The tribes whose names are marked with an asterisk each have more than a dozen species thus far recorded from the West Indies.*

*The tribes which occur in this area are also extensively distributed in the world, and are well represented in the Neotropical Region. In addition, a few African taxa or taxa whose ancestors came from Africa already have been discovered and possibly more will be found. Absence of arboreal Agrina, Eucheila and Inna, and the myrmecophilous Helluonini from the islands is notable. Since the fauna needs much study and new groups are likely to be discovered, a key to carabid adults of the entire Neotropical Region and adjacent areas is provided. Keys are provided to genera of all tribes known to occur on the West Indies and these genera are subsequently annotated. A complete checklist and bibliography are given which cover published accounts and some anecdotal information provided by those now engaged in revisions of the West Indian carabids.*

**SUMMARY**

*La fauna de las Antillas Mayores ha sido estudiada y muestreada ampliamente por P.J. Darlington, Jr., desde sus primeros viajes de campo en 1934 hasta su última publicación sobre carábidos en las islas tropicales en 1970. Las Antillas Menores y las Bahamas no han sido mayormente tomadas en cuenta, por que gran parte de las islas no han sido aún muestreadas. Las siguientes tribus están registradas dentro del área geográfica cubierta por éste estudio, que incluye las Antillas Mayores y Menores, las Bahamas y la mayor parte de las pequeñas islas oceánicas: Carabini; Megacephalini; \*Cicindelini; Enceladini; Pseudomorphini; Scaritini; \*Clivinini; Ozaenini; Brachinini; \*Rhysodini; Trechini; Pogonini; \*Bembidiini; Morionini; \*Pterostichini; Panagaeini; Callistini; Oodini; Licinini; \*Harpalini;*

*Ctenodactylini; Perigonini; Lachnophorini; Cyclosomini; Masoreini; Pentagonicini; Odacanthini; \*Lebiini; \*Zuphiini; Galeritini. Las tribus cuyos nombres están marcados con un asterisco tienen hasta ahora registradas más de doce especies cada una.*

*Las tribus que aparecen en esta área también están ampliamente distribuidas en el mundo y muy bien representadas en la región Neotropical. Además, alguna taxa Africana o taxa cuyos ancestros vienen de Africa han sido ya descubiertos y posiblemente más serán hallados en el futuro. La ausencia de Agrina, Eucheila e Inna arbóreos y de myrmecophilous Helluonini en las islas es resaltante. Ya que la fauna necesita más estudios y que nuevos grupos probablemente serán descubiertos, se suministra una tabla dicotómica para carábidos adultos en toda la región neotropical y áreas adyacentes. También se proporcionan otras tablas para los géneros de todas las tribus que se conocen en las Indias Occidentales y que han sido posteriormente anotados. Se incluye además un listado, una bibliografía y algunas referencias anecdóticas e informes publicados que han sido proporcionados por aquellos actualmente ocupados en las revisiones de los carábidos de las Indias Occidentales.*

## Table of Contents

Introduction .....	352
Classification and Tribes of Terrestrial Caraboidea .....	354
Key to Tribes and Some Genera of Neotropical Carabidae .....	357
Subfamily Carabinae .....	364
Subfamily Scaritinae .....	368
Subfamily Paussinae .....	373
Subfamily Psydrinae .....	376
Subfamily Harpalinae .....	381
Acknowledgements .....	399
Literature Cited .....	400
Appendix A: Checklist of the Species of the West Indies .....	422
Appendix B: Current Revisors of West Indian Genera .....	448
Index to Names of Taxa .....	451

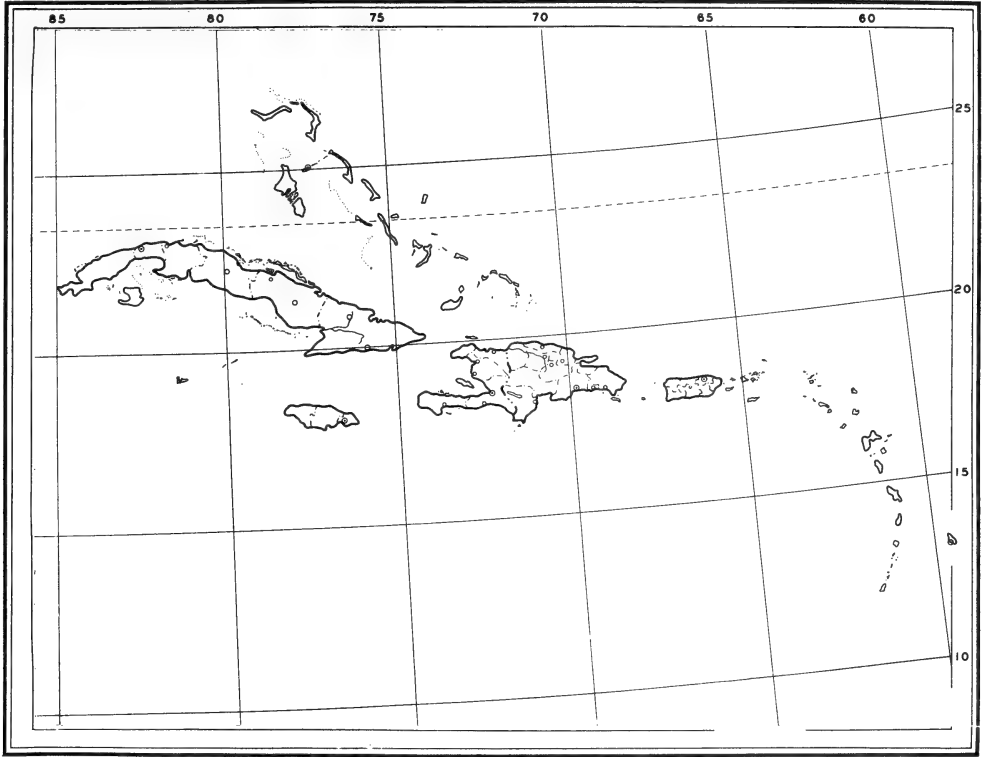
## INTRODUCTION

The fauna of the Greater Antilles was extensively sampled and studied by Darlington (1934, 1935a and b, 1937a and b, 1939, 1941, 1947, 1953, and 1970) although many of the higher mountains remain untouched by carabid collectors. The Lesser Antilles and Bahamas have had far less attention; most islands have not yet been adequately sampled and some not even visited. The following 29 tribes are recorded within the geographic area covered by the study, which includes the Greater and Lesser Antilles, Bahamas, and most smaller islands not on the continental shelf (see Fig. 1): Carabini; Megacephalini; \*Cicindelini; Enceladini; Pseudomorphini; Scaritini; \*Clivinini; Ozaenini; Brachinini; \*Rhysodini; Trechini; Pogonini; \*Bembidiini; Morionini; \*Pterostichini; Panagaeini; Callistini; Oodini; Licinini; \*Harpalini; Ctenodactylini; Perigonini; Lachnophorini; Cyclosomini; Masoreini; Pentagonicini; Odacanthini; \*Lebiini; \*Zuphiini; Galeritini. The tribes whose names are marked with an asterisk each have more than a dozen species thus far recorded from the West Indies.

The tribes which occur in this area are also extensively distributed in the world, and are well represented in the Neotropical Region. In addition, a few African lineages already have been discovered and possibly more will be found. Absence of arboreal *Agrina*, *Eucheila* and *Inna*, other arboreal lebiines, and the myrmecophilous *Helluonini* from the islands is notable.

The purpose of the present paper is to provide a foundation, that is keys, up-to-date checklist, and bibliography for those engaged in generic revisions of the West Indies fauna.





Geographic area covered by this paper and the West Indies Carabid Beetle Project; includes all the Greater and Lesser Antilles, Bahamas, and most smaller islands of the Caribbean not on the continental shelf.

These combined revisions will then provide the basis for a handbook of the fauna that will be dedicated to Philip J. Darlington Jr., who in 1934, stated that someday he wished to revise the West Indian carabid fauna when enough material became available. We hope that the present literature condensation will result in enhancing existing collections of West Indian ground beetles and that these will find their way to the generic revisors listed in Appendix B.

Since the fauna needs much study and new groups are likely to be discovered, a key to carabid adults of the entire Neotropical Region and adjacent areas is provided. Keys are provided to genera of all tribes known to occur on the West Indies and these genera are subsequently annotated. A complete checklist and bibliography are given which cover all published accounts and we provide some anecdotal information provided by those now engaged in revisions of the West Indian carabids. The classification of terrestrial Caraboidea provided herein is based on that given by Erwin (1984). Keys and generic annotations benefited greatly from Reichardt (1977).

## CLASSIFICATION AND TRIBES OF TERRESTRIAL CARABOIDEA

Names in bold face are those of tribes represented in the West Indies

### SUPERFAMILY CARABOIDEA

#### I. Family Trachypachidae

- 01. Tribe Trachypachini
- 02. Tribe Systolosomini

#### II. Family Carabidae

##### Division Nebriiformes

##### A. Subfamily Carabinae

- a. Supertribe Nebriitae
  - 01. Tribe Nebriini
  - 02. Tribe Notiokasini
  - 03. Tribe Opisthiini
  - 04. Tribe Cicindisini
  - 05. Tribe Notiophilini
- b. Supertribe Loriceritae
  - 06. Tribe Loricerini
- c. Supertribe Carabitae
  - 07. Tribe **Carabini**
  - 08. Tribe Ceroglossini
  - 09. Tribe Pamborini
  - 10. Tribe Cychrini
- d. Supertribe Cicindelitae
  - 11. Tribe Collyrini
  - 12. Tribe **Megacephalini**
  - 13. Tribe Ctenostomatini
  - 14. Tribe Mantichorini
  - 15. Tribe **Cicindelini**
- e. Supertribe Omophronitae
  - 16. Tribe Omophronini

## Division Loxomeriformes

## B. Subfamily Scaritinae

- f. Supertribe Migadopitae
  - 17. Tribe Amarotypini
  - 18. Tribe Migadopini
- g. Supertribe Elaphritae
  - 19. Tribe Elaphrini
- h. Supertribe Promecognathitae
  - 20. Tribe Promecognathini
- i. Supertribe Siagonitae
  - 21. Tribe **Enceladini**
  - 22. Tribe Siagonini
- j. Supertribe Hiletitae
  - 23. Tribe Hiletini
- k. Supertribe Pseudomorphitae
  - 24. Tribe **Pseudomorphini**
- l. Supertribe Scarititae
  - 25. Tribe Cnemacanthini
  - 26. Tribe **Scaritini**
  - 27. Tribe **Clivinini**

## C. Subfamily Paussinae

- m. Supertribe Metriitae
  - 28. Tribe Metriini
- n. Supertribe Paussitae
  - 29. Tribe Nototylini
  - 30. Tribe Mystropomini
  - 31. Tribe **Ozaenini**
  - 32. Tribe Protopaussini
  - 33. Tribe Paussini
- o. Supertribe Brachinitae
  - 34. Tribe Crepidogastrini
  - 35. Tribe **Brachinini**

## Division Melaneiformes

## D. Subfamily Broscinae

- p. Supertribe Melaenitae
  - 36. Tribe Melaenini
  - 37. Tribe Cymbionotini
- q. Supertribe Broscitae
  - 38. Tribe Broscini
- r. Supertribe Apotomitae
  - 39. Tribe Apotomini

## Division Psydriformes

## E. Subfamily Psydrinae

- s. Supertribe Psydritae
  - 40. Tribe Gehringiini
  - 41. Tribe Psydrini

- 42. Tribe Melisoderini
- 43. Tribe Tropidopterini
- 44. Tribe Meonidini
- 45. Tribe Patrobini
- 46. Tribe Amblytelini
- t. Supertribe Rhysoditae
  - 47. Tribe **Rhysodini**
- u. Supertribe Trechitae
  - 48. Tribe **Trechini**
  - 49. Tribe Zolini
  - 50. Tribe **Pogonini**
  - 51. Tribe **Bembidiini**
- F. Subfamily Harpalinae
  - v. Supertribe Pterostichitae
    - 52. Tribe **Morionini**
    - 53. Tribe **Pterostichini**
    - 54. Tribe Zabrinini
  - w. Supertribe Panagaeitae
    - 55. Tribe Bascanini
    - 56. Tribe **Panagaeini**
    - 57. Tribe Agonicini
    - 58. Tribe Disphaericini
    - 59. Tribe Peleciini
  - x. Supertribe Callistitae
    - 60. Tribe Cuneipsectini
    - 61. Tribe **Callistini**
    - 62. Tribe Chaetogenyini
    - 63. Tribe **Oodini**
    - 64. Tribe **Licinini**
  - y. Supertribe Harpalitae
    - 65. Tribe **Harpalini**
  - z. Supertribe Dryptitae
    - 66. Tribe Dryptini
    - 67. Tribe **Zuphiini**
    - 68. Tribe **Galeritini**
  - a'. Supertribe Anthiitae
    - 69. Tribe Helluonini
    - 70. Tribe Anthiini
    - 71. Tribe Helluodini
  - b'. Supertribe Orthogoniitae
    - 72. Tribe Idiomorphini
    - 73. Tribe Amorphomerini
    - 74. Tribe Orthogoniini
    - 75. Tribe Catapiesini
  - c'. Supertribe Ctenodactylitae
    - 76. Tribe Hexagoniini

- 77. Tribe **Ctenodactylini**
- 78. Tribe **Calophaenini**
- d'. Supertribe **Lebiitae**
- 79. Tribe **Perigonini**
- 80. Tribe **Lachnophorini**
- 81. Tribe **Graphipterini**
- 82. Tribe **Cyclosomini**
- 83. Tribe **Masoreini**
- 84. Tribe **Pentagonicini**
- 85. Tribe **Odacanthini**
- 86. Tribe **Lebiini**

### Key to Tribes and Some Genera of Neotropical Carabidae <sup>1,2</sup>

- 1 Scutellum concealed by median lobe of posterior margin of pronotum. Intercoxal process of prosternum very broad, covering mesosternum. Body almost circular in outline ..... **OMOPHRONINI**, *Omophron* Latreille, p. 367
- 1' Scutellum visible. Intercoxal process of prosternum not enlarged. Shape of body various ..... 2
- 2 (1') Scape of antenna not evident from dorsal aspect. Head with short, deep antennal sulcus ventrally between eyes and mouthparts. Labium without suture between submentum and mentum ..... **PSEUDOMORPHINI**, *Pseudomorpha* Kirby, p. 369
- 2' Antenna with scape visible from above. Head with or without short deep antennal sulcus ..... 3
- 3 (2') Abdomen with seven or eight sterna normally exposed. Mandible with at least one setigerous puncture in scrobe. Head with one pair of supraorbital setigerous punctures ..... **BRACHININI**, p. 375
- 3' Abdomen with six sterna normally exposed ..... 4
- 4 (3') Clypeus broader than distance between sockets of antennae ..... **CICINDELITAE** ..... 5
- 4' Clypeus narrower than distance between antennal sockets ..... 7
- 5 (4) Metepisternum narrow, sulcate for entire length. Mesepisternum short. Lacinia of maxilla without articulated tooth ..... **CTENOSTOMATINI**, *Ctenostoma* Klug
- 5' Metepisternum plate-shaped, not entirely sulcate. Mesepisternum elongate. Lacinia with articulated tooth ..... 6
- 6 (5') Anterior angles of pronotum more advanced than anterior margin of prosternum. Anterior sulcus of pronotum separated or not from anterior sulcus of prosternum (as well as from prosternal-episternal sulcus). True

<sup>1</sup>Modified from G.E. Ball *In*, Reichardt 1977.

<sup>2</sup>Other genera of the West Indies treated below under tribal discussions; not all Neotropical genera mentioned by name.

	ornamental pubescence absent. Terminal palpomere of maxillary palpus shorter or not than penultimate palpomere .....	
	..... MEGACEPHALINI, p. 366	
6'	Anterior angles of pronotum not more advanced than anterior margin of prosternum. Anterior sulcus continuous from pronotum to prosternum. True ornamental pubescence present in members of most taxa. Terminal palpomere of maxillary palpus longer than penultimate palpomere in members of most taxa .....	CICINDELINI, p. 366
7 (4')	Metasternum without antecoxal suture, almost as long as combined length of abdominal sterna. Front tibia without apical spur (but with pair of prominent apical spines). Antenna moniliform. Head and pronotum deeply grooved .....	RHYSODINI, p. 376
7'	Metasternum with antecoxal suture, and shorter in length. Front tibia with apical spur .....	8
8 (7')	Front tibia with two spurs terminal and ventral, independent of antenna cleaner (latter present or absent) .....	9
8'	Front tibia with one spur apical, one displaced distally, toward antenna cleaner .....	13
9 (8)	Tarsal claws unequal, anterior longer and stronger than posterior. Hind coxae contiguous. Elytron with base marginate to scutellum. Scutellar interneur short .....	CICINDISINI, <i>Cicindis</i> Bruch
9'	Tarsal claws equal. Hind coxae separate. Base of elytron not marginate, or marginate only to lateral constriction .....	10
10 (9)	Hind coxa extended laterally to elytral epipleuron .....	
	..... TRACHYPACHIDAE, SYSTOLOSOMINI, <i>Systolosoma</i> Solier	
10'	Hind coxa normal, not in contact laterally with elytral epipleuron .....	11
11 (10')	Elytron without subapical fold at outer edge. Anterior tibia simple, without longitudinal sulcus or antenna cleaner .....	
	..... NOTOTYLINI, <i>Nototylus</i> Schaum	
11'	Elytron with subapical fold at outer edge. Anterior tibia with antenna cleaner .....	PAUSSITAE, 12
12 (1')	Antenna of 11 clearly visible antennomeres, antennomere 2 distinct, slightly shorter than 3, antennomeres 3 - 11 free, clearly separated and articulated. Anterior coxae not much projected, separated from each other by normal process .....	OZAENINI, p. 374
12'	Antenna of 10 clearly visible antennomeres, antennomere 2 markedly reduced, indistinct. Anterior coxae prominent, contiguous, separated at base, or not, by narrow process .....	PAUSSINI
13 (8')	Anterior coxal cavities open posteriorly .....	14
13'	Anterior coxal cavities closed posteriorly .....	17
14 (13)	Head with two pairs of supraorbital setigerous punctures. Scape of antenna as long as antennomeres 2 - 6 together. Head with short, deep sulcus beneath, between eye and gular region. Mandibles spoon-shaped, each with several teeth .....	HILETINI, <i>Eucamaragnathus</i> Jeannel
14'	Head with single pair of supraorbital setigerous punctures. Scape of antenna normal, less in length than length of antennomeres 2 - 6 together.	

	Mandibles average	15
15 (14')	Frons with series of longitudinal costae. Middle coxal cavities conjunct (entirely enclosed by sterna). Head very broad. Eyes large. Body flat. Size small, length less than 7.0 mm ... NOTIOPHILINI, <i>Notiophilus</i> Duméril	
15'	Frons without series of parallel carinae. Middle coxal cavities disjunct (not entirely enclosed by sterna). Size large, length greater than 10.0 mm	16
16 (15')	Head very narrow (less than half as wide as pronotum at apex). Mandibles elongate, each with two sharp teeth near apex. Labrum long, deeply notched, bilobed ... CYCHRINI, <i>Scaphinotus</i> Latreille	
16'	Head average. Mandibles of normal length, without large teeth near apex. Labrum of normal proportions, apical margin sinuate, but not deeply notched ... CARABINI, p. 365	
17 (13')	Middle coxal cavities disjunct (not entirely enclosed by sterna)	18
17'	Middle coxal cavities conjunct (entirely enclosed by sterna)	21
18 (17)	Antennomeres 2 - 6 with markedly large setae; antennomeres 2 - 4 irregular in shape. Head with two large foveae and deep transverse sulcus behind eyes. Elytron with 12 regular striae ... LORICERINI, <i>Loricera</i> Latreille	
18'	Antennomeres 2 - 6 without markedly elongate setae. Combination of other characters not as above	19
19 (18')	Anterior tibia with both spurs nearly apical. Antenna cleaner, sulcate, confined to posterior surface of tibia, not visible from anterior surface. Body pedunculate ... ENCELADINI, p. 368	
19'	Anterior tibia with one spur markedly preapical, above groove of antenna cleaner, latter in form of notch in antero-lateral surface, visible anteriorly. Body pedunculate or not. Size various	20
20 (19')	Elytron with scutellar stria short (or absent). Body pedunculate ... Supertribe SCARITITAE, p. 369	
20'	Elytron with scutellar stria extended to apex, parallel to elytral suture. Body not pedunculate (in form nebrioid, amaroid, pterostichoid, elongate or ovoid) ... MIGADOPINI	
21 (17')	Scrobe of mandible with one or more setigerous punctures	22
21'	Mandibular scrobe asetose	29
22 (21)	Head with single pair of supraorbital setigerous punctures	23
22'	Head with more than one pair of supraorbital setae	24
23 (22)	Body pubescent. Size small, length of body less than 6.0 mm. Color rufous ... APOTOMINI, <i>Apotomus</i> Illiger	
23'	Body glabrous except for usual fixed setae. Length more than 10.0 mm. Color various, black, coppery, green, but not rufous ... BROSCINI (in part)	
24 (22')	Head with three or more pairs of supraorbital setigerous punctures. Dorsal surfaces of posterior tarsomeres glabrous. Size larger, length of body more than 10.00 mm ... BROSCINI (in part)	
24'	Head with two pairs of supraorbital setae. Dorsal surfaces of posterior tarsomeres each with two or more setae. Size various	25
25 (24')	Penultimate maxillary palpomere pubescent. Frontal grooves more widely	

	separated at middle than at anterior part, and terminated before posterior margins of eyes. Anophthalmous specimens with penultimate maxillary palpomere tumid	26
25'	Penultimate maxillary palpomere glabrous	28
26 (25)	Terminal maxillary palpomere much shorter and more slender than penultimate palpomere. Elytron with base margined. Tarsomeres with dorsal surfaces sulcate longitudinally, or not	BEMBIDIINI, p. 377
26'	Terminal maxillary palpomere normal	27
27 (26')	Elytron with plica posterior to epipleuron. Article 2 of antenna pubescent. Base of elytron margined or not. Each tarsomere with dorsal surface grooved longitudinally or not	ZOLINI
27'	Elytron with internal fold (=plica) not interrupting lateral margin. Antennomere 2 with tuft of setae, only. Base of elytron margined. Dorsal surface of each tarsomere smooth, without longitudinal groove	POGONINI, p. 377
28 (25')	Elytron without internal plica behind epipleuron. Frontal grooves curved: at middle, distance between eye and adjacent groove subequal to distance between grooves, then expanded to genae and ventral side. Glossal sclerite ("ligula") with six or more setae. Male with front tarsomeres 1 - 2 expanded and with tooth apically at inner side	TRECHINI, p. 377
28'	Elytron with internal plica. Frontal grooves at middle more distant from each other than from eyes; grooves not extended behind eyes. Glossal sclerite with two or three setae. Three or four basal front tarsomeres of male slightly and symmetrically expanded and rounded to apex (or simple)	PSYDRINI
29 (21')	Terminal maxillary palpomere articulated obliquely with penultimate palpomere. Integument markedly punctate. Head and pronotum either with pubescence thick and long, or completely glabrous, and surface brilliant, metallic. Elytron with well developed plica	PANAGAEINI, p. 385
29'	Terminal and penultimate maxillary palpomeres articulated in straight line, at apex of penultimate palpomere. Integument punctate or not, setose or not. Elytron with or without plica	30
30 (29')	Head with more than two pairs of supraorbital setigerous punctures. Lateral edge of pronotum with several setae. Anterior tibia extended latero-apically as prominent, thick tooth-like projection	CNEMACANTHINI, <i>Cnemalobus</i> Guérin-Mènèville
30'	Head without, or with one or two pairs of supraorbital setigerous punctures. Number of pronotal setae various. Form of front tibia various	31
31 (30')	Antennomeres 3-10 each with apical ring of long setae, each seta longer than antennal scape. Labrum elongate, anterior margin projected as broadly rounded lobe. Mentum and submentum fused, mental suture not evident; mentum-submentum bilobed posteriorly, each lobe with three or more long setae. Penultimate labial palpomere long, with numerous setae. Glossal sclerite slender, projected well beyond apices of paraglossae, with four or more apical setae	



- ..... CHAETOGENYINI, *Camptotoma* Reiche
- 31' Antennomeres 3-10 with apical setae shorter than scape. Combination of characters other than as above ..... 32.
- 32 (30') Head without or with one pair of supraorbital setigerous punctures ..... 33
- 32' Head with two pairs of supraorbital setigerous punctures ..... 40
- 33 (32) Elytron with apical margin truncate. Body glabrous and shining, depressed. Head without or with one pair of supraorbital setigerous punctures. Pronotum without, or with one pair of setigerous punctures at posterior angles ..... CATAPIESINI
- 33' Elytron with apical margin not truncate. Body various. Head with one pair of supraorbital setigerous punctures. Pronotum with one or two pairs of setigerous punctures ..... 34
- 34 (33') Elytron without internal plica near apex ..... 35
- 34' Elytron with internal plica ..... 38
- 35 (34) Antennomere 3 with few setae only, not pubescent, antennomere 4 pubescent in apical 0.33 ..... 36
- 35' Antennomere 3 pubescent in apical 0.33, antennomere 3 pubescent throughout ..... 37
- 36 (35,60) Body rotund, elytra vaulted. Elytron with deep interneurs. Mandibles and maxillae elongate. Mentum of labium shallowly bisinuate, with short tooth ..... PTEROSTICHINI, *Cyrtolaus* Bates
- 36' Body average, elytra normal. Striae of elytra average. Mouthparts not as above ..... PTEROSTICHINI, Agonina (part), p. 383
- 37 (35') Terminal maxillary palpomere elongate, more than twice length of penultimate palpomere. Terminal labial palpomere glabrous, not elongate. Antennomeres of flagellum quadrate ..... PTEROSTICHINI, *Cratocerus* Dejean
- 37' Terminal maxillary and labial palpomeres similar in size and proportions. Antennomeres of flagellum slender, elongate, antenna filiform ..... HARPALINI, p. 388
- 38 (34') Surface of elytra and pronotum finely and densely punctate, with fine pubescence. Scutellar interneur normal ..... CALLISTINI, p. 386
- 38' Dorsal surface not densely punctate, without fine pubescence. Scutellar interneur short or absent ..... 39
- 39 (38') Elytron with interval 9 almost absent; interneur 8 in form of deep, rugose groove, especially from middle onward; scutellar interneur short; epipleuron gradually tapered to apex. Terminal palpomere (maxillary or labial) normal ..... OODINI, p. 386
- 39' Elytron with interval 9 normal, wider or narrower; interneur 8 normal, similar to others; scutellar interneur absent, epipleuron expanded near mesothoracic region, then tapered gradually posteriorly ..... PELECIINI, *Pelecium* Kirby
- 40 (32') Antennomeres 5 - 10 submoniliform, short or slightly depressed. Margin of pronotum with approximately seven pairs of setae. Interneur 8 in form of zigzag sulcus, with numerous scattered setigerous punctures. Body

	subpedunculate. Legs flattened	MORIONINI, p. 381	
40'	Antennomeres 5 - 10 slender, antenna distinctly filiform; or submoniliform and pronotum with single pair of lateral setae; and/or other character states different from above		41
41 (40')	Elytron with internal plica		42
41'	Elytron without internal plica		43
42 (41)	Penultimate labial palpomere plurisetose	ZABRINI, <i>Amara</i> Bonelli	
42'	Penultimate labial palpomere bisetose		
		PTEROSTICHINI (part), p. 382	
43 (41')	Pronotum narrow, distinctly longer than wide, at apex as wide as posterior part of head		44
43'	Pronotum not distinctly longer than wide, and/or wider at apex than posterior part of head		47
44 (43)	Terminal maxillary and/or labial palpomere trianguloid. Tarsomere 4 notched, bilobed		45
44'	Terminal maxillary and labial palpomeres cylindrical, normal. Tarsomere 4 bilobed or entire		46
45 (44)	Terminal labial palpomere trianguloid. Antenna with scape and antennomere 3 of about same length. Tarsal claws pectinate		
		LEBIINI, <i>Agra</i> Fabricius	
45'	Terminal maxillary and labial palpomeres trianguloid. Scape of antenna very large, longer than antennomere 3. Tarsal claws smooth		
		DRYPTINI, <i>Neodrypta</i> Basilewsky	
46 (44')	Tarsomere 4 deeply notched at apex, bilobed, lobes more than 0.5 length of tarsomere 5. Elytra entire, abdominal terga completely covered		
		CTENODACTYLINI, p. 392	
46'	Tarsomere 4 simple or only slightly emarginate apically. Elytron with apex truncate		
		ODACANTHINI, p. 395	
47 (43')	Posterior tibia with inner spur more than 0.5 length of hind basitarsus inner spur longer than outer spur. Tarsal claws pectinate or not		48
47'	Posterior tibia with spurs more or less equal and shorter than 0.5 length of hind basitarsus		50
48 (47)	Labrum elongate, length more than 0.5 width at base. Head markedly constricted posteriorly, in form of neck. Pronotum widest at base, narrowed anteriorly		
		LEBIINI, <i>Nemotarsus</i> LeConte	
48'	Labrum average, length less than 0.5 width at base. Head not constricted posteriorly in form of neck. Pronotum either widest anteriorly, with sides slightly sinuate before base, or base and apex about equal, and sides rounded		49
49 (48')	Pronotum with sides sinuate posteriorly. Dorsum of elytra variegated, or predominantly dark with pale spots. Spurs of middle and hind tibia with serrate margins, each tibia with spines of average length. Each mandible with dorsal and ventral margins basally projected laterally about equally. Antenna with each of flagellomeres 5-10 about twice as long as wide		
		CYCLOSOMINI, p. 394	
49'	Pronotum with sides rounded or nearly straight, not sinuate. Dorsum of		

- elytra uniformly rufous, rufo-piceous, or piceous, same color as head and pronotum. Spurs of middle and hind tibia with margins smooth. Each mandible basally with dorsal margin extended laterally as broad, shelf-like projection. Flagellomeres 5-10 each not more than 1.25 times as long as wide ..... MASOREINI, p. 394
- 50 (47') Labrum appearing elongate (actually about quadrate). Head with one pair of setae ventrally, posterior to submentum. Elytron with penultimate umbilicate seta nearer margin than those adjacent ..... LEBIINI, *Pericalina*, p. 397
- 50' Labrum transverse, distinctly wider than long. Head without or with one pair of setae ventrally, posterior to submentum. Elytron with penultimate umbilicate seta in various positions ..... 51
- 51 (50') Elytron with apical margin truncate ..... 52
- 51' Elytron with apical margin entire, sinuate or not ..... 58.
- 52 (51) Tarsal claws pectinate ..... LEBIINI (part), p. 395
- 52' Tarsal claws with inner margins smooth, not pectinate ..... 53.
- 53 (52') Dorsal surface glabrous, except for normal fixed setae. Antennomeres 1-3 glabrous, except one long seta on scape, and ring of setae near apex of antennomeres 2 and 3 ..... 54
- 53' Dorsal surface finely pubescent. Antennomeres 1-3 pubescent ..... 56
- 54 (53) Labial palpomere 3 acuminate apically. Elytron with dorsal surface markedly iridescent. Legs flavous ..... LACHNOPHORINI, *Eucaerus* LeConte, p. 394
- 54' Labial palpomere 3 subtruncate to truncate apically, not acuminate. Elytron with dorsal surface iridescent or not. Legs flavous or darker ..... 55
- 55 (54') Pronotum approximately pentagonal in shape, with sides sharply constricted posteriorly. Head markedly constricted posteriorly. Mentum and submentum fused, mental suture not evident ..... PENTAGONICINI, *Pentagonica* Schmidt-Goebel,
- 55' Pronotum with sides not markedly constricted posteriorly. Head markedly constricted or not posteriorly. Mentum and submentum fused or separated by distinct suture ..... LEBIINI (part), p. 395
- 56 (53') Size small, length of body about 6.0 mm., or less. Scape of antenna longer than combined length of antennomeres 2 plus 3 ..... ZUPHIINI, p. 390
- 56' Size larger, length of body 10.0 mm or more. Antennal scape shorter or longer than combined length of antennomeres 2 plus 3 ..... 57
- 57 (56') Antennomeres 5-11 more or less flattened, finely pubescent, central area each side generally triangular and more or less glabrous ..... HELLUONINI
- 57' Antennomeres 5-11 not flattened, uniform pubescent ..... GALERITINI, p. 391
- 58 (51') Clypeus sloped downward, surface more or less concave, emarginate anteriorly. Labrum deeply notched ..... LICININI, p. 387
- 58' Clypeus plane, not sloped, anterior margin straight or slightly emarginate. Labrum with anterior margin truncate or slightly concave ..... 59
- 59 (58') Elytron with interneur 8 impressed and obliquely extended almost to apical

	sutural angle. Posterior trochanter almost 0.5 length of posterior femur	...
	.....	PERIGONINI, p. 393
59'	Interneur 8 normal. Length of posterior trochanter various	60
60 (59')	Dorsal surface glabrous, except for some scattered setae	36
60'	Dorsal surface more or less pubescent	61
61 (60')	Elytron with odd-numbered intervals setose	...
	.....	PTEROSTICHINI, Agonina (part), p. 383
61'	All elytral intervals setose	62
62 (61')	Elytral interneurs more deeply impressed on anterior half; and-or anterior half of interneurs coarsely punctate and poster half finely punctate or impunctate. Setae erect and at least a few longer, as on scape	...
	.....	LACHNOPHORINI (part), p. 393
62'	Elytron with interneurs equally punctate, impressed or not. Body with short, dense and decumbent, pubescence	...
	.....	PTEROSTICHINI, Agonina (part), p. 383

#### A. SUBFAMILY CARABINAE

Van Emden (1942), following older authors, accepted the traditional division of Carabidae into the Carabinae and Harpalinae, and within the latter studied and redefined the tribes with a seta in the mandibular scrobe ("Harpalinae Piliiferae", as opposed to the "Harpalinae Impilae", with glabrous mandible). In his characteristically thorough study, van Emden defined the taxonomic position of several inadequately known genera. Crowson (1955:5,6) who also distinguishes these two groups, and gives subfamilial rank to a third, the Scaritinae, considers the Brachinini, normally placed as a distinct subfamily, in Harpalinae; he does not mention the pseudomorphines.

Lindroth (1961:13; 1969b:xii) fused the classically accepted subfamilies Carabinae and Harpalinae. Lindroth (1969b:xvii-xxi) justified his action well enough, and there is no need to go into details here. However, it should be mentioned that, in a general way, the Carabinae correspond to the "Caraboidea Simplicia", and the Harpalinae to the "Caraboidea Limbata" of Jeannel's system (1941, 1942a) which was followed by Ball (1960:91-92).

Herein only those anisochaetes with glabrous, styliform parameres or a derivation of such a paramere are considered Carabinae. In some groups, like the Carabini, the distance between the two spurs is very small, thus the Carabinae excludes most tribes of Carabidae. Based on a system proposed by Kryzhanovsky (1976) and Erwin (1979, 1984, 1985) and several new ideas presently under discussion by carabidologists, a provisional classification into Divisions, Subfamilies, Supertribes, and Tribes is used here.

The Nebriiformes include phylogenetically some groups of water beetles, but we have followed tradition and not covered those groups here (see Erwin, 1985), restricting our comments to only the Subfamily Carabinae.

#### SUPERTRIBE CARABITAE

This subtribe presently contains four tribes, only one of which is found in the West Indies.

## TRIBE CARABINI

In South America, carabines are included in two genera, *Calosoma* Weber and *Ceroglossus* Solier, each with few species. In temperate regions of the Northern Hemisphere, the tribe is represented by many species, most of which are included in *Calosoma sensu lato*, and *Carabus* Linné. Adults of most species are large, and many are elegant in form and color. This elegance has attracted the attention of unskilled commercially oriented amateurs who have caused substantial confusion at generic, specific and subspecific levels by "playing" with the taxonomy, often for their own profit.

Lapouge (1929b-1931) recognized five subtribes: Ceroglossina, Aplothoracina (a monobasic subtribe for an endemic genus of Saint Hélène [see Basilewsky, 1972]), Calosomina, Carabina, and Cychrina. The last-named group is generally ranked now as a tribe.

Larvae of both Neotropical genera are known (van Emden, 1942:22-23).

## Key to Genera of West Indian Carabini

- 1        Antennomeres 2 and 3 carinate. Mandibles at least basally with transverse ridges. Labrum black. Elytra with humeri well developed (hind wings normally developed), or sloped (hind wings reduced) ..... *Calosoma* Weber, p. 365
- 1'       Antennomeres 2 and 3 cylindrical, not carinate. Mandibles smooth, or finely punctate. Labrum black or metallic. Elytra with humeri sloped (hind wings reduced) ..... *Carabus* Linné, p. 365

*Calosoma* Weber, 1801. A genus worldwide in distribution, with many named species, subspecies, varieties, and aberrations. The genus has been the subject of two important world revisions: Breuning (1927-1928b) and Jeannel (1940). The Nearctic and Neotropical species were treated also by Gidaspow (1959, 1963). The genus was handled very differently by these authors, thus a universally accepted system has not been adopted. Breuning recognized 20 subgenera; Jeannel recognized 20 genera. Gidaspow recognized a single genus, with the Neotropical species arrayed in five subgenera.

Lindroth (1961:42 and following), in his study of the Canadian fauna, eliminated the subgenera of *Calosoma*, recognizing informal taxa designated as "species groups". In part, these coincide with the subgenera of previous authors.

Larvae and adults of *Calosoma* are predators of lepidopterous larvae. According to Lindroth (1961:44), most adults are strong fliers, coming from great distances at the time of mass eclosion of caterpillars. Two species have been recorded from the West Indies.

*Carabus* Linné, 1758. This is a Holarctic genus, with maximum divergence and richness in eastern Asia. It is represented in mesic mountain forests of México by two species whose adults are brachypterous: *C. forreri* Bates, confined to the Sierra Madre Occidental and the Chiricahua Mountains of southeastern Arizona, and *C. hendrichsi* Bolivar, Rotger and Coronado, confined to several peaks in the Sierra Madre Oriental. *Carabus basilicus* Chevrolat of Puerto Rico, the only *Carabus* listed for the islands, is a doubtful record and needs confirmation.

## SUPERTRIBE CICINDELITAE

The systematic position of the Cicindelitae among the family Carabidae has been very much discussed. In spite of some exceptions, such as Mandl (1971:507-508) who suggests returning the group to the status of a distinct family, most modern authors have considered tiger-beetles a subfamily of Carabidae. Crowson (1967:109, 1981:694), who had originally (1955) considered the 'Cicindelinae' as a subfamily of Carabidae, suggested that the absence of urogomphi and ligula in larval tiger-beetles, adult labrum usually with more than six setae, and position of the front tibial spurs in adults support familial status for tiger beetles. Although not as yet published, Kavanaugh (pers. comm.) and other sources (e.g. Jeannel, 1946:106) indicate that numerous structural features suggest that the Cicindelitae is the sister group of Carabidae, that the complex is very old, and that the tiger beetle lineage became highly adapted to the hunt through specialization of mouthparts and ambulatory parts, and of course the larvae have adapted a unique prey capture technique and acquired or modified those features necessary for this. Here the group is considered part of the Carabidae, within present day usage of that taxon. A reclassification, potentially splitting Carabidae into many families, must await considerable amounts of study.

Horn (1910) proposed arrangement of the 'Cicindelinae' in two groups, Alocosternales (=Collyrinae Csiki, 1906) and Platysternales (=Cicindelinae Csiki, 1906). The genera of Alocosternales were arranged in two tribes, Ctenostomatini (=Ctenostomini auct.) and Collyrini. Of these only Ctenostomatini have Neotropical representatives: Collyrini are Oriental and Australian. The genera of Platysternales were arranged in the tribes Mantichorini (a small group of deserticolous species from southern Africa), Megacephalini, and Cicindelini. Each of these tribes was divided into subtribes. Many species, especially of *Cicindela*, have numerous "varieties" and "subspecies", which certainly are not more than individual variants or population ecophenotypes.

The West Indian fauna is comprised of 2 genera and 18 species.

## TRIBE MEGACEPHALINI

*Megacephala* Latreille, 1802. This is a diverse, worldwide genus with numerous Neotropical species. Horn (1910:130ff) arranged the species in several groups, which might be used as subgenera. Basilewsky (1966:13-14) suggested, in a revision of the African species, that at present it is not possible to divide the genus. Three species of *Megacephala* occur in the West Indies.

## TRIBE CICINDELINI

*Cicindela* Linné, 1758. This is a highly diverse, worldwide genus, with nearly 700 species. In Horn's concept, the genus is quite homogeneous, but more recently authors (especially of the "French school" and followed by the American amateurs) have split the genus. Jeannel (1946:43ff) was the first author to propose the splitting, limiting himself to the species of Madagascar. In a series of papers, Rivalier (1950:217ff; 1954:250ff; 1961:121ff; 1963:30ff), dismantled *Cicindela*, recognizing 55 genera, most of which he described as new. Schilder (1953:539-576), recognized 17 genera, synonymizing several of the names previously proposed by Rivalier (1950). Rivalier's work is based exclusively on structure of the internal sac of the

aedeagus; Schilder's system is presently without any morphological basis. Rivalier (1954) studied the Neotropical species (including several species from southeastern United States) placing them in the following "genera" which should be regarded perhaps as species groups to bring them in line with the rest of the carabids, providing thus a more balanced system.

*Cylindera* Westwood, 1831. Thirty species, (eight in Brazil) placed in two subgenera: *Cylindera s. str.* and *Plectographa* Rivalier, 1954.

*Cicindelidia* Rivalier, 1954. Forty-six species distributed from the United States, Mexico, through Central America to the west of South America.

*Habroscelimorpha* Dokhtoureff, 1883. Ten species ranging from the United States to Venezuela and the Antilles.

*Eunota* Rivalier, 1954. A single species in the United States.

*Microthylax* Rivalier, 1954. Three species in Mexico and Cuba.

*Opilidia* Rivalier, 1954. Five species whose aggregate range extends from Central America to Colombia and Venezuela.

*Brasiella* Rivalier, 1954. Twenty-three species distributed from Mexico to Argentina, of which 11 are recorded from Brazil. Rivalier (1955:77ff) revised the *argentata* group of this "genus", describing three new species and several new subspecies.

*Ellipsoptera* Dokhtoureff, 1883. Restricted to the United States, with nine species.

*Dromochorus* Guérin-Ménéville, 1845. With two Texan species.

The species of *Cicindela s. lat.* typically inhabit open area, especially river margins and sea beaches, however numerous of them may also be found in tall grass. Adults fly readily. A total of 15 species, arrayed among some of the genera above, have been recorded from the West Indies.

## SUPERTRIBE OMOPHRONITAE

This supertribe contains a single tribe, the Omophronini.

### TRIBE OMOPHRONINI

The single genus of this tribe is *Omophron* Latreille, 1802. Most of the species are in the Holarctic Region, a few are in the Oriental Region. Several species, included in the subgenus *Stenomophron* Semenov-Tian-Shanskij, 1922, occur in Mexico; three occur in Central America, but are typical Nearctic elements; there is no Neotropical lineage. A single species, *Omophron dominicensis* Chaudoir, 1868a, was described from Santo Domingo, in the Greater Antilles, however Nichols (pers. comm.) informs us that this probably is a South African species that was mislabelled and that no *Omophron* species is indigenous to the West Indies.

Adults are distinctive in appearance because the body is so rotund. Larvae and adults live in bare sandy areas, near bodies of either standing or flowing water. During the day, adults hide in burrows in soil, or under stones near the water's edge. They are easily dislodged by splashing their hiding places with water.

Bänninger (1921) and Semenov-Tian-Shanskij (1922) revised the world fauna of this subtribe. Benschoter and Cook (1956) revised the species of North America. Nichols (MS) using modern methods has studied the entire genus, especially those species of the New World.

## SUBFAMILY SCARITINAE

The new contents of this subfamily are based on studies of Erwin and Stork (1984) and Erwin (1985).

## SUPERTRIBE SIAGONITAE

Only one tribe of this group occurs in the New World. Specimens of *Siagona* in the Museum in Paris labelled Venezuela and seen by one of us (TLE), appear to be mislabelled.

## TRIBE ENCELADINI

Erwin (1978b) regarded this tribe as part of the Sigonitae based on both adult and larval characteristics, but maintained a tribal status for *Enceladus* based on larval features, recognizing full well that the genus *Luperca* appears to be intermediate in adult structures. Members of the single species of *Enceladus* are found under bark of large trees in South America. Recently, a single specimen was collected on Montserrat, B.W.I., thus the tribe is now known from the West Indies.

*Enceladus* Bonelli, 1813, which includes the single species *E. gigas* Bonelli (1813:460).

## SUPERTRIBE PSEUDOMORPHITAE

This predominantly Australian supertribe (five genera), also has one genus in the Oriental Region, one in Africa, and one in the Western Hemisphere. Notman (1925) published a worldwide revision of the group, in which the genera are clearly defined, however the relationships among these are poorly understood and a modern revision is sorely needed. Erwin (1985), based on newly discovered characteristics, hypothesizes that this group belongs in the Scaritinae.

## TRIBE PSEUDOMORPHINI

Most authors have considered the Pseudomorphini as a distinct subfamily, because of its very special characteristics. In recent years, only Crowson (1955:5, 6) did not give them such special status, apparently including them in the Harpalinae, together with Brachininae and thus following Jeannel (1941). The Harpalinae are considered a distinct subfamily by most authors.

Little is known about habits of Pseudomorphitae. Moore (1964), who described the first larva of the subtribe (of the Australian genus *Sphallomorpha*), described also the habits of adults of certain Australian genera, frequently found in association with ants. The larvae he described were collected in brood chambers of *Iridomyrmex*. There are few references about species of *Pseudomorpha*. Ogueta (1967:230) refers to a specimen of *P. lacordairei* (Dejean & Boisduval, 1829) collected in a termite nest, and Lenko (1972) collected larvae (in cocoons), pupae, and adults of *P. laevissima* Chaudoir, 1852 in nests of the ant species *Camponotus rufipes*. The larva of *Pseudomorpha*, only briefly described by Lenko, is similar to that of *Sphallomorpha*. Erwin (1981), in a synopsis of the supertribe, described larvae of *Pseudomorpha* and discussed all that is presently known of the group. According to Moore



(1964:246), larval characters of this group stress separation of Brachininae and Pseudomorphini in Balteifera, as originally suggested by Jeannel (1942a:1102). However, Erwin (1981) discussed phylogenetic relationships based on adult characteristics and believed the group should be classified near the Scaritini.

*Pseudomorpha* Kirby, 1825 (= *Heteromorpha* Kirby, 1825; = *Axinophorus* Dejean & Boisduval, 1829; = *Drepanus* Dejean, 1831), which includes 20 species in the United States and Mexico, one in Haiti and six in Brazil and Argentina.

### SUPERTRIBE SCARITITAE

According to Erwin (1985), the Scarititae is presently composed of three tribes, two of which reach the West Indies. Both the Scaritini and Clivinini are found as soil burrowers or at least running on top of the ground. The Morionini, a group of carabids found in decaying logs, have often been placed in this taxon. However, members of Morionini have closed middle coxal cavities, glabrous parameres, and the larva has an inner lobe (setiferous) on the maxilla, thus Erwin (1985) placed it in the Pterostichitae as a separate tribe and we follow that placement here. Larval characteristics need to be evaluated phylogenetically for the family in order to determine apotypy, thus the placement is still provisional.

#### Key to Tribes of West Indian Scarititae

- 1 Tarsomere 5 with unguitractor plate extended as setiform process between claws ..... Clivinini, p. 371
- 1' Tarsomere 5 with unguitractor plate not extended as setiform process ..... Scaritini, p. 370

#### Key to Subtribes of West Indian Scarititae

- 1 Antennal scape with single preapical setigerous puncture ..... 2
- 1' Antennal scape asetose ..... 3
- 2 (1) Elytron with lateral series of umbilicate punctures reduced to two groups of 0-3 punctures behind humerus and before apex ..... *Dyschiriina*, *Dyschirius* Bonelli, p. 371
- 2' Elytron with lateral series of umbilicate punctures either not interrupted or at least not markedly so ..... Clivinina (= *Ardistomina*), p. 371
- 3 (1') Mentum with median tooth longer than lateral lobes, extended obliquely dorsad almost to ventral surface of labrum. Mandibles edentate, falcate, slender. Head with one or more pairs of supraorbital setigerous punctures ..... Forcipatorina, p. 373
- 3' Mentum with tooth subequal in length to lateral lobes, not extended dorsad. Mandibles with large teeth basally. Head with single pair of supraorbital setigerous punctures ..... Scaritina, p. 370

## TRIBE SCARITINI

Scaritini occur in all major zoogeographical regions; genera are numerous, and several genera are rich in species. There are no recent revisions of the Neotropical Scaritini as a whole, except for Bänninger's world monograph of the Scaritina (see below). Even the subdivisions of the tribe are not well established; many genera have not been critically studied in recent years, so their position herein must be considered provisional. Members of the Scaritini are generally large to very large beetles; the males have multisetiferous parameres, and the unguitractor plate of the terminal tarsal segment is not setiform.

One subtribe of Scaritini in the old sense, the Scapterina, has usually been listed for the Neotropical Region with one genus, *Listropus* Putzeys, 1863. However, *Listropus* is now regarded as a subgenus of *Schizogenius* Putzeys (Whitehead and Reichardt, 1977), thus they are in the following tribe, Clivinini. The Scapterina are thus not represented in the New World (see also Jeannel 1946:220).

## SUBTRIBE SCARITINA

A large, cosmopolitan subtribe, with usually large members, many of fossorial habits, and with brachypterous or apterous adults. One genus, with several subgenera, has been recorded in the West Indies.

### Key to Subgenera of West Indian *Scarites*

- 1 With ventral "strigae". Clypeus of most specimens with one pair of setigerous punctures. Pronotum with postangular seta and at least one anterior. Metasternum of most specimens with one or more setigerous punctures ..... 2.
- 1' Without ventral "strigae". Metasternum of most specimens asetose ..... 3
- 2 (1) Metasternum, behind middle coxae, as long or longer than hind coxae. Frontal sulci not narrow and deep in most specimens, confused with the longitudinal rugosity between eyes ..... *Distichus* Motschulsky, p. 370
- 2' Metasternum of most specimens much shorter than hind coxae. Head with frontal sulci shallow, between supra-orbital setae usually with coarse punctures and longitudinal rugae. Prosternal process of most specimens punctate and setose. Middle tibia of most specimens with second tooth more or less developed ..... *Taeniolobus* Chaudoir, p. 371
- 3 (1') Mandibles with dorsal surface striate ..... *Scarites s. str.* Fabricius, p. 370
- 3' Mandibles with dorsal surface smooth ..... *Antilliscaris* Bänninger, p. 371

*Scarites* Fabricius, 1801. This is a highly diverse, cosmopolitan genus, whose species are arrayed in several subgenera. Only four of these occur in the Neotropical Region, all of which have West Indian representation. Seven species in total are known to occur in the West Indies.

*Distichus* Motschulsky, 1857 (= *Lophogenius* Motschulsky, 1857; = *Scaritodes* Chaudoir, 1879; = *Adialampus* Gozis, 1882; = *Dischistus* Portevin, 1929). Species of this subgenus occur in the Old World and in the Neotropical Region from Mexico to Argentina, including the West Indies). There are 17 Neotropical species (revision: Bänninger, 1938).

*Taeniolobus* Chaudoir, 1855 (= *Pleurogenius* Motschulsky, 1857; = *Stigmaterus* Motschulsky, 1857; = *Scaris* Chaudoir, 1879). This subgenus includes African, Oriental, and Neotropical species (including a Cuban species).

*Scarites* s. str. (= *Parallelomorphus* Motschulsky, 1850; = *Pharamecomorphus* Motschulsky, 1857). Species of *Scarites* live in almost all zoogeographical regions; in the New World there are species from the United States to Argentina, and also in the West Indies (revision: Bänninger, 1938).

*Antilliscaris* Bänninger, 1949. The three species of this endemic West Indian subgenus are known only from Puerto Rico (Hlavac, 1969; Darlington, 1970).

### TRIBE CLIVININI

The subtribe Ardistomina is here combined with Clivinina, because relationships among their respective genera are not known. Kult (1950) limited the Ardistomina to *Ardistomis*, *Aspidoglossa* and *Neoreicheia*, as genera with dilated male protarsi, but this probable plesiotypic characteristic is not stable even among these lineages; also, the key characteristics used to distinguish *Neoreicheia* (reduced eyes and enlarged genae) occur in various *Ardistomis* s. str. These three genera along with *Oxydrepanus* and such Old World genera as *Reicheia*, *Syleter*, and allies probably do form a monophyletic radiation, but even if that is so its precise relationship to other Clivinina is not known. Some workers have assigned *Schizogenius* and *Solenogenys* to the Ardistomina, but the former is a clivinine and the latter a salcediine (= Forcipatorina, see below).

The isolated position of *Dyschirius* and allies, usually assigned to the Clivinina, was discussed by Bruneau de Miré (1952) and Whitehead (1969), with the conclusion that they belong to a separate subtribe, Dyschiriina, of unclear affinity. We choose here to include them in the Clivinini and note that they may constitute a separate tribe.

### SUBTRIBE DYSCHIRIINA

See Whitehead (1969) for discussion of contents, characteristics, and general distribution of this subtribe. Kult (1950) recognized two genera for the Neotropical species that he studied: *Akephorus* LeConte and *Dyschirius* Bonelli. Lindroth (1961:137) treated the two groups as congeneric, but they probably should be regarded as distinct genera. South American species referred to *Akephorus* by Kult (1950) belong to *Dyschirius*, subgenus *Dyschiridius* Jeannel (Whitehead, 1969).

*Dyschirius* Bonelli, 1813. Primarily of Megagaeon distribution, most of the species of this diverse genus are in the Nearctic and Palaearctic Regions. However, 18 described species are represented in the American tropics, with a known aggregate range extending as far southward as the Pampas of Argentina. No satisfactory subgeneric classification has been proposed. Members of *Dyschirius* live on bare clay or sand, often near water. Adults and larvae, so far as known, prey on staphylinids of the genus *Bledius*, and on heterocerids (Lindroth 1961:137).

### SUBTRIBE CLIVININA

This is a highly diverse subtribe, with numerous genera and species. The group was studied by Putzeys (1846; 1863; 1866), but there is no general recent revision. Several genera



species of subgenus *Listropus*. One species has been recorded from the West Indies.

*Oxydrepanus* Putzeys, 1866. A genus of minute members, exceedingly diverse in aedeagal structure, doubtless related to *Neoreicheia*, and probably belonging to the ardistomine radiation. Two species have been recorded from the West Indies.

*Ardistomis* Putzeys, 1846 (with subgenera *Ardistomis* s. str. and *Semiardistomis* Kult, 1950. *Ardistomiellus* Kult, 1950, is a junior synonym of *Semiardistomis*). *Ardistomis* is exclusively American, with 11 species occurring in the Antilles.

*Aspidoglossa* Putzeys, 1846. A New World genus with 25 Neotropical species (distributed from southeastern United States to northern Argentina and Antilles), of which three have been recorded from the West Indies.

#### SUBTRIBE FORCIPATORINA (=OXYSTOMINA)

This is a small subtribe of Clivinini which occurs predominantly (and possibly exclusively) in the Neotropical Region. Two Oriental genera have to be restudied before their inclusion in the group is warranted. The species of the subtribe, placed in six genera (Jorge de Silva, MS) are exclusively South American, with a single species of *Stratiotes* Putzeys, known from the Lesser Antilles (Martinique and Dominica). Recent studies by Erwin and Stork (in prep) have shown that the members of Salcediina constitute the sister group of *Stratiotes*, thus the two subtribes, Forcipatorina and Salcediina, will be merged.

#### SUBFAMILY PAUSSINAE

At present it is well established that paussids are true Carabidae (the first author to verify the fact seems to have been Burmeister, 1841:76). Kolbe (1927:205; 1930:16) definitively related the Paussini to Ozaenini, having been followed by more recent authors (Darlington, 1950; Crowson, 1955; Basilewsky, 1962; Lindroth, 1969b:xxi). Other authors, e.g. Jeannel (1941:89; 1946:45, 46), even though accepting the relationships between the two, continued to consider the Paussidae as a distinct family, thus accepting a polyphyletic classification. Crowson (1955:6; 1981:694) considered the group at family level, including in it the "Ozaeninae".

Recent work on defense chemicals, and structure of the defense mechanism (Eisner *et al.*, 1977, Moore 1979) and reanalysis of data in Erwin 1970 (Erwin 1979) show that the bombardier beetles, Brachinidae, have a sister group relationship with the Ozaenine/Paussine lineage. Erwin (1979) included the Metriitae and Nototylini in the Paussinae, however, neither of these groups occur in the West Indies.

#### SUPERTRIBE PAUSSITAE

Darlington (1950) arranged the paussids in three tribes, the Protopaussini, Paussini and Ozaenini. Protopaussini, of which very little is known, is a primitive tribe restricted to the Oriental Region. Paussini are myrmecophiles. Each species apparently occurs with a different species of ant, and the hosts are known to belong to the tribes Myrmicini or Camptonotini. Carvalho (1959) records several African species of *Paussus* in *Pheidole* nests (Myrmicini). Jeannel (1946) found no relationship between the classification systems of these ants and carabids, although this should be restudied with modern methods. In South America, only one

species has been found thus far in an ant nest (*Monacis*, Dolichoderini). Very little is known about the life history of the third tribe, the Ozaenini, but *Physe*a adults and larvae have been collected from nests of *Atta* (Attini), the leaf-cutting ants. Adults of other genera have been collected from beneath bark of fallen trees or, at night, on logs.

Wasmann (1929) described 20 fossil species from Baltic amber (end of Eocene or beginning of Oligocene), which he placed in seven genera, of which only *Arthropterus* is present in the recent fauna (of Australia). Darlington (1950:85) suggested that Wasmann exaggerated the number of both genera and species (all based on single specimens). Unfortunately, a restudy of these fossils has not been undertaken.

### TRIBE OZAENINI

This tribe includes 14 genera (Bänninger, 1927) which occur in the Australian, Oriental, Ethiopian (including Madagascar) and Neotropical Regions (a few species occur in southwestern United States). Only the genus *Pachyteles* has been recorded in the West Indies.

Little is known about the habits of Ozaenini. Adults of some genera of the Oriental Region were collected in decaying wood: at least one species of *Physe*a (possibly *Physeomorpha* as well), has myrmecophilous habits. Larvae are only known of *Physe*a and *Pachyteles* (van Emden, 1942:24-25). Adults of several genera occurring in Central and South America are "bombardiering" beetles. All aspects of this activity are like those of *Brachinus* and *Pheropsophus*, except the droplets are released from side turrets (flange of Coanda) rather than a medial one.

*Pachyteles* Perty, 1830. This is the richest and most diverse Neotropical genus of the tribe, with at least 50 species (plus two in the southern United States); two have been recorded from the West Indies. There is no revision of the genus, and identification of the species is nearly impossible. A larva of one species from Guatemala was collected from beneath bark (van Emden, 1942:59).

### SUPERTRIBE BRACHINITAE

This group is usually separated from the rest of the carabids because of the number of normally visible abdominal sterna of adults. All other carabids have six, but brachinine females have seven and males have eight. This structure is correlated with the "bombarding" mechanism, i.e., the capacity to eject volatile substances through a small opening in front of tergum IX. The larger number of exposed segments permits more mobility of the abdomen, permitting the droplets of volatile substance to be aimed toward a target (Eisner, 1958).

Because of this defense mechanism of adults, Brachinitae are known as "bombardier beetles". This behaviour is not restricted to this supertribe, having been recorded for other tribes as well (e.g. *Galerita*, see below; *Agra*, see Erwin, 1979; Ozaenini, see above), however the unique structures are restricted. There is also an old reference that helluonine adults have the capacity to bombard, but this has not been confirmed in recent years (Reichardt, 1974b:221-222). Reichardt (1971a) recorded bombarding behaviour for *Pheropsophus aequinoctialis* and *P. rivieri*, and it is known that both *Pheropsophus* and *Brachinus* adults are true bombardiers.

Erwin (1970), following Ball (1960), considered this supertribe as a division, Brachinidae, with the genera arranged in two tribes, Crepidogastrini (restricted to the southern parts of



*Clinidium* s. str.. This subgenus is well represented in the Neotropical Region, with 11 species endemic in the Antilles (most described as new by Bell, 1970).



*Plesioglymmius* Bell and Bell, 1978. The range of this genus is disjunct, with one area including the Greater Sunda Islands and Mindanao, and the other Brazil and Cuba. There are a number of undescribed species (Bell, pers. comm.). One species has been reported from the West Indies.

## SUPERTRIBE TRECHITAE

This supertribe is comprised of several tribes, all of which have rather small members. The groups are diverse in habitat and structure and occur in most habitable areas of the world.

### TRIBE TRECHINI

This is a tribe of small carabids of worldwide distribution, but with predominance of genera and species in the cold and temperate parts of the World (distribution similar to that of *Bembidion*). In features of life history, the taxa are organized in two groups, one with subterranean habits (usually cavernicolous species with reduced eyes) and a terricolous group (with well-developed eyes). A small subgroup of the latter are marine species, which live among rocks in the intertidal zone. In the Neotropical Region, marine species are only known from southern South America. In the tropical parts of the continent relatively few species are known, possibly because they occur in habitats rarely adequately collected, i.e. deep humus and soil.

Larvae of Neotropical species are unknown; those from the Old World are well known (van Emden, 1942:28-30).

### SUBTRIBE PERILEPTINA

*Perileptus* Schaum, 1860a. A genus of Old World origin, perhaps African, characterized by pubescent eyes of adults. Only four Antillean species are known.

### TRIBE POGONINI

This is a tribe of eight genera according to Csiki (1928), especially of the Old World, with halophilous species whose members are encountered along sea shores or at the margins of salt lakes. Chaudoir (1871b) studied the whole group; the two genera occurring in the Neotropical Region were recently studied by Reichardt (1974a). Immature stages are only known for Old World species (van Emden, 1942:17).

*Diplochaetus* Chaudoir, 1871b. Two species in the United States, one in México and one in the Antilles and northern South America (also recorded from Brazil). Members live on coastal and lowland saline beaches. Adults are nocturnal.

### TRIBE BEMBIDIINI

A tribe of worldwide distribution and predominant in all regions of both hemispheres. The tribe is well represented in southern South America, especially by *Bembidion*; Central America and the Antilles have many species, some with clear Nearctic relationships. The tropical species of South America have not been studied in recent years and are rarely found in collections. In recent years this fauna, especially the Tachyina, has been studied by Erwin (1971b, 1973,

1974a, 1974b, 1975, 1978a). *Bembidion*, with fewer tropical species and more temperate ones has been studied by Erwin and Kavanaugh (1980, 1981) and Erwin (1982). Jeannel (1962) studied the fauna of the southern parts of South America; unfortunately he recognized too many genus-group taxa without clear affinities. Thus, this fauna is still in need of a thorough revision.

The habits of Bembidiini are varied. Members of Bembidiina are mostly riparian or seabeach species; a few occur near inland ponds and at the edges of wet alkalie sloughs. Anillina includes tiny endogean, anophthalmous individuals which live in deep humus in upland habitats. Several new species were recently discovered in Guatemala using sifting and berlese methods; many more will doubtless be found throughout the Neotropical Region. Tachyina are the most diverse of the tribe. These rather small beetles occur as arboricoles, in wood and under bark, epigeal and hypogean, near water of all kinds, on sea beaches, and near other salt deposits. Several live among epiphytes in the forest canopy. Larvae are known for *Tachyta* and *Mioptachys* (Erwin, 1975) and probably for *Xystosomus* (Erwin, 1973; van Emden, 1942).

#### Key to Subtribes of West Indian Bembidiini

- |    |  |   |
|----|--|---|
| 1  | Front tibia truncate, not notched apico-laterally  | 2   |
| 1' | Front tibia obliquely and markedly notched apico-laterally   | 3   |
| 2  | (1) Abbreviated scutellar interneur present; recurrent groove of elytral apex absent   | Bembidiina, p. 381  |
| 2' | Abbreviated scutellar interneur absent; recurrent groove of elytron present  | Tachyina, in part ( <i>Xystosomus</i> and <i>Mioptachys</i> ), p. 380 |
| 3  | (1') Body pale and generally pubescent; with or without eyes, If with eyes, then head somewhat withdrawn into pronotum   | 4   |
| 3' | Body pale or dark, with fixed tactile setae only; eyes present; head not withdrawn into pronotum   | Tachyina, p. 379  |
| 4  | (3) Labrum deeply notched and covering mandibles; elytral apices soft, separated at suture, and more or less truncate; flight wings and eyes present in most adults      | Tachyina, in part ( <i>Lymnastis</i> and <i>Micratopus</i> ), p. 381  |
| 4' | Labrum entire and not covering mandibles; elytral apices normal, not soft, held together at suture (in adults of many species) and rounded; flight wings and eyes absent | Anillina, p. 378  |

#### SUBTRIBE ANILLINA

Jeannel (1937, 1963) published two monographs on this group. Although mostly occurring in temperate zones, few representatives are in the Neotropical Region. Taglianti (1973) studied the Mexican species and Erwin (1982) reviewed the Central American species. It is most probable that the paucity of the tropical fauna is due to the lack of collections from suitable habitats.

*Stylulus* Schaufuss, 1882 (= *Petrocharis* Ehlers, 1884). A monobasic genus from the Virgin Islands and southeastern United States, originally described in Colydiidae. It is highly likely that several species are extant, but have not been collected. We doubt that the species from the Virgin Islands is conspecific with the mainland United States form(s).

## SUBTRIBE TACHYINA (INCLUDING MICRATOPINA, =LIMNASTINA)

A diverse subtribe which, until very recently, was chaotic from the taxonomic point of view. Most authors have considered Micratopina (=Limnastina) a distinct group, but Erwin (1974a) united this assemblage with Tachyina. Jeannel (1962) studied the Tachyina (*sensu stricto*) of the southern tip of South America and described a few new genera. Erwin (1974b) redefined the genera, synonymizing some names proposed by Jeannel, and published revisions of several genera (Erwin, 1973, 1974b, 1975). Most new World genera occur in the West Indies, therefore a complete key is given below.

**Key to Genera of Neotropical Tachyina (modified from Erwin, 1974a; see Erwin, 1974b, for elytral setal codes)**

- 1 Elytron impunctate, with eight longitudinal carinae extended from base to apex. Pronotum with five carinae. Head with three carinae. .... *Costitachys* Erwin
- 1' Elytra, pronotum and head non-carinate or, elytra carinate-punctate. .... 2
- 2 (1') Mentum without deep foveae, with or without shallow depressions on each side ..... 3
- 2' Mentum with two deep foveae, each circular or horseshoe-shaped ..... 8
- 3 (2) Front tibia almost or perfectly truncate at apex ..... 4
- 3' Front tibia markedly oblique apico-laterally ..... 5
- 4 (3) Elytral disc without setae Ed2-6. Specimen convex ..... *Xystosomus* Schaum
- 4' Elytral disc with setae Ed3 and 5 Convex or depressed, with markedly reflexed pronotal margins ..... *Miopotachys* Bates, p. 380
- 5 (3') Elytra and abdominal sterna sparsely pubescent, remaining parts of body of most adults also pubescent: Color testaceous or flavo-testaceous. Head slightly or markedly retracted into pronotum. Recurrent stria of elytron absent or indistinctly marked ..... 6
- 5' Elytra and abdominal sterna not pubescent. Testaceous or black. Head not retracted into pronotum. Recurrent stria distinctly marked ..... 7
- 6 (5) Sternum VI of both sexes with four long setae along posterior margin, lateral setae falciform ..... *Micratopus* Casey, p. 381
- 6' Sternum VI with long, erect setae: male with two, female with four ..... *Lymnastis* Motschulsky, p. 381
- 7 (5') Recurrent stria of elytron short, curved, closer to suture than to lateral margin. Form convex or subdepressed ..... *Elaphropus* Motschulsky, p. 380
- 7' Recurrent stria elongate, straight, very close to lateral margin. Form usually depressed ..... *Tachyta* Kirby, p. 380
- 8 (2') Recurrent stria elongate, extended anteriorly beyond seta Ed6, and from there curved backward, hook-shaped ..... 9
- 8' Recurrent stria short, curved, not extended beyond seta Ed6, or elongate, and near lateral margin ..... 10
- 9 (8) Elytral interneur 8 subsulcate beyond middle, with apical portion of sulcus

- curved medially behind setae Ed5 and 6. Recurrent stria in form of hook around Ed6 ..... *Paratachys* Casey, p. 381
- 9' Elytral interneur 8 subsulcate, but not curved medially next to Ed5 and 6. Recurrent stria in form of hook around Ed6 or erased near Ed6 ..... *Tachys* Stephens, p. 381
- 10 (8') Pronotum without posterior angles. Form pedunculate. Interneur 8 externally absent ..... *Liotachys* Bates
- 10' Pronotum with posterior angles, or at least not with pedunculate form. Interneur 8 complete, or at least present anteriorly and/or posteriorly ..... 11
- 11 (10') Elytral interneurs erased or indistinctly striate. Form small and depressed or subdepressed. Testaceous or flavous .... *Polyderis* Motschulsky, p. 381
- 11' Elytral interneurs punctate or sulcate-striate ..... 12
- 12 (11') Elytral interneur 8 of most adults with post-humeral fovea(e) in basal fourth or in middle: or elytra with eight completely punctate interneurs ..... *Pericompsus* LeConte, p. 380
- 12' Elytral interneur 8 non-foveolate, nor elytron with more than five interneurs externally visible ..... *Meotachys* Erwin

*Mioptachys* Bates , 1882 (= *Tachymenis* Motschulsky, 1862, junior homonym of *Tachymenis* Wiegmann, 1835. For details, see Erwin, 1976). A predominantly Neotropical genus (12 named species, four in Brazil), with a single species in the Nearctic Region. Three species have been recorded in the West Indies.

*Tachyta* Kirby, 1837. A Holarctic genus. *T. hispaniolae* Darlington, 1934, occurs in the Antilles and *T. nana inornata* Say, 1825 ranges south to Belize. Revised by Erwin (1975).

*Elaphropus* Motschulsky, 1839 (= *Tachylopha* Motschulsky, 1862; = *Tachyura* Motschulsky, 1862; = *Barytachys* Chaudoir, 1868b; = *Sphaerotachys* Müller, 1926; = *Trepanotachys* Alluaud, 1933; = *Tachyphanes* Jeannel, 1946). A predominantly Holarctic genus, with numerous species in the Old World, several in the Nearctic, and 10 or so in the Neotropics. Two species have been recorded in the West Indies.

*Pericompsus (sensu lato)* LeConte, 1851 (= *Tachysops* Casey, 1918a = *Tachysalia* Casey, 1918a = *Leiotachys* Jeannel, 1962 = *Leptotachys* Jeannel, 1962). In his recent revision of the genus, Erwin (1974b) arranged *Pericompsus* in three subgenera, two Neotropical and *Upocompsus* Erwin in the Australian Region. Three species have been recorded in the West Indies.

The two Neotropical subgenera are distinguished as follows:

- 1 Interneur 8 with deep almost perforate fovea, in middle of elytron or slightly in front of middle. Each elytron also with two subhumeral, variously placed foveae. Setae Eo4 in position "d" ..... *Pericompsus (sensu stricto)*, p. 380
- 1' Interneur 8 without fovea in or near middle. Foveae posterior to humeri shallow, each with seta, or small, perforated, in basal 0.25, next to seta Eo4c; or foveae absent ..... *Eidocompsus* Erwin, p. 380

*Eidocompsus* Erwin, 1974b. With 13 Neotropical species, of which one is known from the West Indies.

*Pericompsus (sensu stricto)*. With 46 species, of which 6 are known from the West Indies.

*Tachys* Stephens, 1828b (= *Isotachys* Casey, 1918a). A Nearctic genus, with several species in México, Guatemala, and Antilles. Three species have been recorded on the West Indies.

*Paratachys* Casey, 1918a (= *Eotachys* Jeannel, 1941). A worldwide genus, with hundreds of Neotropical species, almost totally undescribed. These are predominantly from México, Central America, and Antilles, but several are known from Brazil and other countries. Nine species have been recorded in the West Indies.

*Polyderis* Motschulsky, 1862 (= *Microtachys* Casey, 1918a = *Neotachys* Kult, 1961 = *Polyderidius* Jeannel, 1962). Worldwide, with four species in Central America and one in the Antilles.

*Lymnastis* Motschulsky, 1862 (= *Limnastis* auct. = *Paralimnastis* Jeannel, 1932). With most of its species in the Old World, this genus is represented in the New World by a single species, *L. americana* Darlington, from Cuba.

*Micratopus* Casey, 1914a (= *Blemus* LeConte, 1848, not Stephens). As redefined by Erwin (1974a), this New World genus includes two Antillean species.

### SUBTRIBE BEMBIDIINA

A highly diverse subtribe and taxonomically complex. This group needs to be restudied and Erwin and Kavanaugh (1980, 1981) and Erwin (1982) have begun their monographic treatment of the subtribe.

Very few species are known from tropical parts of the Neotropical Region, however many species do occur in the tropical highlands, especially in the West Indies.

*Bembidion* (*sensu lato*) Latreille, 1802 (= *Bembidium* auct.). A worldwide genus, subdivided in a large number of subgenera, with 10 described species known from the West Indies. The *vernale* group (Erwin, 1982) has undergone radiation on the mountain systems of the larger islands just as it has in the highlands of Central America.

### SUBFAMILY HARPALINAE

This subfamily is here defined as those groups whose members possess conjunct mesocoxae and conchiferous male parameres without setae (as an apotypic state).

### SUPERTRIBE PTEROSTICHITAE

This supertribe must surely be the largest and most disparate of the family. Not only have many groups been dumped here based on gross similarity, but many other groups, rather non-similar in appearance, have been included. The group as a whole is inadequately known systematically.

### TRIBE MORIONINI

This is a tribe of about 10 genera (Csiki, 1929:479), mostly of the tropics of the Old and New Worlds. Most authors have considered the Morionini as a subtribe of Pterostichini (an action even maintained by Straneo, *in litt.*), but more recently it has been considered as a distinct tribe, of uncertain relationships. Whitehead & Ball (1975), discussing relationships of

the groups within Pterostichini, exclude Morionini and Catapiesini from the tribe. Here it is regarded as a tribe, following Erwin (1984), somewhat intermediate between the psydrines and *Cratocerus* and company of Pterostichini. Larval characteristics indicate strong relationship with the pterostichines, even though some features tend to resemble those of certain scaritine larvae (cf. Thompson, 1977, 1979; Jorge-Silva and Costa, 1983).

As far as known, adults and immatures of Morionini live in fallen logs and adults have well developed wings. Van Emden (1953b:51-54) described and discussed the presumed larva of *Morion orientale* Dejean, comparing it to a larva which he earlier (1942:27) had referred to the scaritine genus *Scarites*, subgenus *Distichus*, but in reality was that of *Morion cordatum* Chaudoir, (cited as *Morion georgiae* Palisot). Reichardt reared the larva of *Morion brasiliense* Dejean. Two genera occur in the New World, only one of which is found in the West Indies.

*Morion* Latreille, 1810 (= *Morio* auct.). A genus of worldwide distribution, with several Neotropical species (one from the Antilles).

### TRIBE PTEROSTICHINI (INCLUDING AGONINI)

The Pterostichini is one of the most diverse groups of Carabidae and likely the last of an old stock which gave rise to many of the higher carabid groups. It has many taxa which are typically cold-temperate (in South America represented in the southern part of the continent) and others tropical. It seems that Pterostichina are commoner in colder and more temperate climates, being replaced by Agonina in the tropics.

The Neotropical fauna is taxonomically difficult. One of the problems is divergence in generic concepts, e.g. the Jeannel (splitting) *versus* the more conservative (lumping) concept. Many monobasic or very small genera have not been properly studied and compared with each other, and their status and systematic position remains unsettled. On the other hand, there are markedly diverse worldwide "genera" such as '*Pterostichus*' and '*Colpodes*', both of which are paraphyletic, if not polyphyletic.

Part of the confusion arises from Csiki's world catalog of Carabidae (Csiki, 1929; 1930; 1931). Several of the groups included in the tribe have already been eliminated from it by subsequent authors. These are:

(1) The subtribe Morionini (Csiki, 1929:474-484), at present considered a distinct tribe by many authors and here included as such.

(2) The subtribes Meonidi (Csiki, 1929:484), Melisoderi (*ibidem*:485-486), Tropidoptera (*ibidem*:486-491) and Psydri (*ibidem*:494), were all fused to form the tribe Psydrini, and the Nomiini are considered a separate tribe. Although none of these are present in the West Indies, the included checklist ranks these groups as full tribes after Erwin (1984).

(3) The subtribe Catapiesi (Csiki, 1929:492-493), is now also considered a distinct tribe of Lebiitae.

With these groups eliminated, there still remains the bulk of genera in the tribe, and the confusion is great; it is impossible to identify the natural system now.

A second problem is arrangement of genera in subgroups or even limits of the tribe. One of the highly diverse groups within this tribe is the Agonina, which has been accorded very different status by different authors. Csiki (1931:739) considered them as a subtribe of his Pterostichini, and has been followed by such authorities as Lindroth (1966:441). Ball (1960:129) preferred to consider the Agonini as a distinct tribe, but in a more recent paper (Whitehead & Ball, 1975:595) returned the agonines to Pterostichini, and did the same with

another group here considered as a distinct tribe (the Lachnophorini). Their action, in relation to the Agonina, was justified by the fact that they fused a genus of true Pterostichini with a genus normally considered agonine (see the subtribe Cyrtolaina).

Lindroth's (1966) arrangement of the Pterostichini is restricted to the Nearctic fauna, not including the several tropical groups. Here, Whitehead & Ball (1975) are followed, with the inclusion of Caelostomina and the exclusion of the Lachnophorini.

#### Key to the Subtribes and Genera of West Indian Pterostichini

- 1        Scutellar interneur absent ..... 2
- 1'       Scutellar interneur present ..... 4
- 2 (1)   Anterior tibia markedly dilated apically; antennomeres 4-10 quadrate,  
about as wide as long ..... Caelostomina, *Caelostomus* MacLeay, p. 384
- 2'       Anterior tibia not dilated much apically; antennomeres 4-10 longer than  
wide, filiform ..... 3
- 3 (2')   Dorsal surface metallic blue, copper, or green .....  
..... Euchroina, *Dyschromus* Chaudoir, p. 384
- 3'       Dorsal surface not metallic, piceous or rufous, often spotted and/or  
iridescent ..... Loxandrina, *Loxandrus* LeConte, p. 385
- 4 (1')   Elytron with internal plica near apex .....  
..... Pterostichina, *Pterostichus* (*sensu lato*), p. 384
- 4'       Elytron without internal plica near apex ..... 5
- 5 (4')   Anterior tibia externally canaliculate and male aedeagus basally melanistic  
..... *Glyptolenus* Bates, p. 384
- 5'       Anterior tibia not canaliculate; male aedeagus melanistic or not ..... 6
- 6 (5)   Tarsomere 4 of anterior tarsus emarginate; male aedeagus melanistic  
(except in some depigmented species); head not constricted behind eyes ..  
..... *Agonum* Bonelli, p. 384
- 6'       Tarsomere 4 of anterior tarsus lobate; male aedeagus not melanistic; head  
somewhat constricted behind eyes ..... *Platynus* Bonelli, p. 384

#### SUBTRIBE AGONINA (=ANCHOMENINA; =PLATYNINA)

This is a markedly diverse group of predominantly temperate distribution. As discussed above, some authors prefer to consider the Agonina as a tribe distinct from the Pterostichini, but recent studies indicate close relationship to the extent they must be considered as members of the same tribe.

Whitehead & Ball (1975), considering the agonines as a subtribe of Pterostichini, separate the Agonini (in the old sense) in three subtribes, the Agonina, Sphodrina, and Pristosiina. The Sphodrina include mainly troglobites, and are restricted to the Holarctic Region and New Zealand. Barr originally described the genus *Mexisphodrus* (Barr, 1965:66) as a Neotropical representative of the Sphodrina, but later concluded that the genus is better placed among the true Agonina (Barr, 1970, 1973).

The Agonina have numerous tropical representatives. The group is not well understood, and only in a few recent papers has Whitehead started to settle the status of the Mexican (and other Neotropical) species. The neotropical species are very inadequately known, their immature

stages not at all.

*Platynus* (*sensu lato*) Bonelli, 1810. Whitehead (1973) studied the Mexican species formerly placed in *Colpodes* and *Agonum* (as well as in other smaller genera), and resurrected *Platynus* Bonelli from synonymy with *Agonum* Bonelli, 1810, for the Mexican forms. Nonetheless, classification of Mexican *Platynus* is far from settled, much less that of other Neotropical species; according to Whitehead (*l.c.*:214) there are more than 100 undescribed species from México. Presently, it is the largest genus in the West Indies with 55 species recorded.

*Agonum* Bonelli, 1810. Also a highly diverse, cosmopolitan genus, predominantly in temperate areas. Possibly it is not in the Neotropical Region; subgenera and species groups are numerous in other faunas. Excluding *Rhadine*, *Hemiplatynus*, *Stenoplatynus* and *Platynella*, (see *Platynus*, above) from *Agonum*, there remain only species placed in *Agonum* (*sensu stricto*): five evidently Nearctic species which reach into México and the Antilles, as well as 37 species which occur in México (nine) and the Antilles (one), as also in South America-Chile (nine), tropical parts (18), of the latter six in Brazil. Of the subgenus *Anchomenus* Bonelli, (also a predominately temperate group), there are four Nearctic species which also occur in México and the Antilles, three exclusively Mexican and two from Colombia.

*Glyptolenus* Bates, 1878 (= *Glyptoglenus* Bertkau, 1878). Originally a predominantly Central American genus, *Glyptolenus* was recently studied by Whitehead (1974), who included in it several species formerly placed in *Colpodes* or *Platynus*, and which now includes 17 species, predominantly South American, of which six are recorded from Brazil, one from Jamaica and two from the Lesser Antilles.

#### SUBTRIBE EUCHROINA

A small Neotropical subtribe (which also includes the Australian *Setalis* Laporte) of metallic-colored adults, some of large size. Four genera are currently placed in this subtribe.

*Dyschromus* Chaudoir, 1835. Restricted to México (five species) and the Antilles (five species).

#### SUBTRIBE PTEROSTICHINA

This subtribe, which includes most genera and species of Pterostichini, is taxonomically complex and not understood. One of the great problems is the highly diverse, worldwide genus *Pterostichus* Bonelli, with many subgenera (frequently considered genera, e.g. by Straneo (1979), who considers some the Neotropical subgenera as genera, and excludes *Pterostichus* from the Neotropical Region).

*Pterostichus* Bonelli, 1810. This is a very large Holarctic genus, comprised of many subgenera and species groups. Species of *Pterostichus* *s. str.* may or may not occur in the West Indies. Two are listed as such, one of which is a *Poecilus* species and the other may be incorrectly assigned to this genus.

#### SUBTRIBE CAELOSTOMINA

*Caelostomus* MacLeay, 1825. This predominately African and Oriental genus is represented in the West Indies by a single introduced species, *C. punctifrons* Chaudoir, from



## SUBTRIBE LOXANDRINA

## SUPERTRIBE PANAGAEITAE

TRIBE PANAGAEINI

*Quaest. Ent.*, 1984, 20 (4)



exotic Oodini.

At the generic and specific level, the "Oodides" were monographed in a posthumous work of Chaudoir (1882a, 1882b). In this work, there was no inclusion of keys to genera, only characterizations of the latter and placement of the species in different groupings.

Very little is known about the Neotropical species of Oodini. Members of the tribe live in swamps and marshes, along water courses, and on the forest floor, in leaf litter, in the lowlands. Larvae are known for few exotic species (van Emden, 1942:43-44).

### Key to Genera and Subgenera of West Indian Oodini

- |        |   |   |
|--------|---|---|
| 1      | Clypeus with pair of setigerous punctures antero-laterally .....  | 2 |
| 1'     | Clypeus without setigerous punctures .....  | 3 |
| 2 (2)  | Labrum with three setae along anterior margin .....   |   |
|        | ..... <i>Anatrichis</i> , subgenus <i>Oodinus</i> Motschulsky, p. 387                                       |   |
| 2'     | Labrum with six (or five) setae along anterior margin .....   |   |
|        | ..... <i>Oodes</i> Bonelli, p. 387  |   |
| 3 (1') | Labrum with six setae along anterior margin. Size small, length of body <i>ca.</i> 7.0 mm .....             |   |
|        | ..... <i>Anatrichis</i> ( <i>sensu stricto</i> ) LeConte, p. 387  |   |
| 3'     | Labrum with three setae along anterior margins. Size various, but length of body not less than 9.0 mm ..... |   |
|        | ..... <i>Stenocrepis</i> Chaudoir, p. 387   |   |

*Oodes* Bonelli, 1810. This is a moderately diverse and probable polyphyletic genus, with species in most zoogeographic regions. The New World fauna is small; three species occur in the United States, and possibly three in the Neotropical Region, one of which was recorded from the West Indies.

*Stenocrepis* (*sensu lato*) Chaudoir, 1857. This is a moderately diverse temperate-tropical New World endemic genus, with Nearctic, Middle, and South American species. Members are associated with streams, large rivers, and in marshes in open areas. The species are arranged in three subgenera, with seven species recorded from the West Indies:

*Stenocrepis* (*sensu stricto*). This subgenus includes 16 Neotropical species which range from Mexico and the West Indies to Brazil.

*Stenous* Chaudoir, 1857. The distribution pattern is similar to that of *Stenocrepis*, with 12 species.

*Crossocrepis* Chaudoir, 1857. This subgenus includes two species: one in México, and one in the West Indies.

*Anatrichis* (*sensu lato*) LeConte, 1853. This genus includes seven Neotropical species, whose collective ranges extend from Brazil to northern México. The species are arrayed in two subgenera, *Oodinus* Motschulsky and *Oodiellus* Chaudoir, at present. Possibly, these groups should be ranked as genera. Two species have been recorded from the West Indies.

### TRIBE LICININI

This is a moderately diverse and divergent tribe, distributed in all of the major zoogeographical regions of the world, each region with one or more endemic genera. In the New World, the group is represented by two elements: a Holarctic temperate-tropical component, including *Diplocheila* Brullé, *Dicaelus* Bonelli, and *Badister* Clairville; and a southern hemisphere component represented by *Eutogeneius* Solier. Ball (1959) revised the Nearctic

species, providing a firm foundation on which to study the world fauna.

*Diplocheila* Brullé, 1834a. This wide-ranging Megagean genus is represented in the New World by the endemic *straitopunctata* group of subgenus *Isorembus* Jeannel. Of the eight Nearctic species, one, *D. major* LeConte, inhabits also the northern fringe of the Neotropical Region, but only on the island of Cuba.

SUPERTRIBE HARPALITAE

This supertribe contains at present only the following tribe.

TRIBE HARPALINI

This is one of the more highly diverse tribes of the family (as are Pterostichini and Lebiini), and also much in need of taxonomic revision. Although the tribe seems not well represented in the South American tropics, species of some genera are numerous. Some genera, as in the stenolophines, are more diverse and divergent in the Palaearctic areas, and for these groups South America is zoogeographically marginal.

The supra-generic classification is not yet settled. A first attempt at a reclassification was that of van Emden (1953a), which was followed later by various authors. Noonan (1973) revised the genera of Anisodactylina, and in 1976, he presented a synopsis of the genera of Harpalini of the world, grouping them in four subtribes. This scheme is used here, though it is recognized that some of the subtribes may not be monophyletic.

Little is known about life histories and immature stages of Neotropical species. Van Emden (1942:39-43) described larvae of *Anisotarsus* (at present considered a subgenus of *Notiobia*), *Trichopselapus*, *Barysomus*, and *Acupalpus*. Nègre (1963:210) refers to larvae of *Polpochila* (described by Chu, 1945).

Key to Subtribes of West Indian Harpalini

- 1        Penultimate labial palpomere bi- or trisetose ..... Stenolophina, p. 388
- 1'      Penultimate labial palpomere plurisetose ..... Harpalina, p. 389

SUBTRIBE STENOLOPHINA (=CRATOCARINA, BRADYCELLINA OF AUTHORS)

A subtribe of more temperate distribution, and represented in the tropics by only a few genera. Noonan (1976) gave the tribe a new definition, including in it elements of various different groups.

Key to Genera of West Indian Stenolophina

- 1        Mentum with tooth ..... 2
- 1'      Mentum without tooth ..... 3
- 2 (1) Head with frontal impressions deep, long, extended posteriorad of hind margin of eye; elytron without sutural interneur; pronotum with posterior margin with complete transverse groove ..... *Pogonodaptus* Horn, p. 389
- 2'      Head with frontal impression shallower, shorter; if extended laterad,

- groove terminated near front margin of eye ..... *Bradycellus* Erichson, p. 389
- 3 (1') Elytron with posterior series of umbilicate punctures not divided into two groups of four punctures each ..... *Acupalpus* Latreille, p. 389
- 3' Elytron with posterior series of umbilicate punctures divided into two groups of four punctures each ..... *Stenolophus* Stephens, p. 389

*Bradycellus* (*sensu lato*) Erichson, 1837 (= *Acupalpus* Thomson, not Latreille). Of the eight subgenera cited by Ball (1960:86), only two have Neotropical representatives. However, the species are not well understood, and many remain to be described. Further work might reveal previously unrecognized species groups. Four species have been recorded in the West Indies.

*Acupalpus* Latreille, 1829. A markedly diverse, worldwide genus, whose species are arranged in several subgenera. The Neotropical species (including those of West Indies) have not been properly studied, and their subgeneric position is uncertain. Two species have been recorded in the West Indies.

*Stenolophus* Stephens, 1827. Also a markedly diverse, worldwide genus. Csiki (1932a:1259) considered it to be a subgenus of *Acupalpus*: more recent authors give it generic rank. Thirteen described Neotropical species are included, distributed from Middle to South America, but only two of these have been recorded in the West Indies.

*Pogonodaptus* Horn, 1881. A genus with only three species, one ranging from Central America to Texas, one in Panamá, and one in Haiti. At least two of these species live in marshes and swamps.

## SUBTRIBE HARPALINA

This is the most diverse of the harpaline subtribes, and also the most diverse of the Neotropical groups. According to van Emden (1958), only the Selenophori, whose males have the ostium of the aedeagus located dorsally, are represented in South America. Noonan (1976) places the Neotropical genera in two groups, the Selenophori and the Amblystomi.

### Key to Genera of West Indian Harpalina

- 1 Elytron with interneurs 2, 5, and 7 impunctate ..... *Harpalus* Latreille
- 1' Elytron with at least interneur 2 with several small setigerous punctures ..... 2
- 2 (1') Elytron with interneur 7 impunctate on discal portion, interneur 5 with or without setigerous punctures ..... *Stenomorphus* Dejean, p. 390
- 2' Elytron with setigerous punctures in interneurs 2, 5, and 7 ..... 3
- 3 (2') Head enlarged, clypeus with anterior margin distinctly concave, basal membrane of labrum narrowly exposed; elytra iridescent ..... *Amblygnathus* Dejean, p. 390
- 3' Head average, anterior margin of clypeus straight or only very slightly concave; luster of elytra various, iridescent or not ..... 4
- 4 (3') Elytral intervals more or less densely setigerously punctate, or rugulose ..... *Athrostictus* Bates, p. 390
- 4' Elytral intervals impunctate, smooth ..... *Selenophorus* Dejean, p. 390

### The Harpali Group

Primarily a Megagean group with two genera represented in México, but not in the Neotropical Region. Of these, *Euryderus* LeConte, a monobasic genus, containing *E. grossus* Say, is known in México only from northern Sonora. *Harpalus* Latreille is represented in the deserts and mountains of northern México, in the Trans-Volcanic Sierra, and in the mountains of Oaxaca. About 15 species are in Mexico, several of which are undescribed. The group in México is maximally diverse and divergent in the Sierra Madre Occidental. One species of *Harpalus* is known from the West Indies, but in light of the above this species may be mis-assigned.

### The Selenophori Group

*Selenophorus* Dejean, 1829 (= *Gynandropus* Dejean; = *Hemisopalus* Casey; = *Celiomorphus* Casey; = *Selenalius* Casey). A markedly diverse Nearctic and Neotropical genus, much in need of revision. Nearctic species were arrayed in subgenera by Casey (1914b); Noonan (MS) synonymized *Gynandropus*. In the Neotropics there are 142 described species, of which 28 are known from the West Indies; the 'group' *Gynandropus* Dejean has 12 species in Middle and South America, two of which are known from the West Indies. The species of the genus inhabit a wide variety of habitats, such as grassland and deserts. A few species are synanthropic occurring in tropical gardens, yards, and under sidewalks.

*Amblygnathus* Dejean, 1829. A genus comprising about 20 species (nine described) from the West Indies (one species), Middle America, and northern South America. Mexican members inhabit the environs of *Sagittaria* and *Typha* marshes. The group is close to *Selenophorus*, and perhaps should be treated as a subgenus.

*Athrostictus* Bates, 1878 (= *Arthrostictus* auct.). This is a moderately divergent group, with some 16 species, one of which is known from the West Indies. The species inhabit lowlands; in México and Central America, individuals are found in drier, open forests. Some are synanthropic.

*Stenomorphus* Dejean, 1831 (= *Agaosoma* Ménétries). Revised by Darlington (1936), it comprises 10 species, most of which are in mainland Middle and northern South America. Two species (*S. manni* Darlington and *S. cubanus* Darlington) occur in the West Indies.

## SUPERTRIBE DRYPTITAE

This supertribe has three tribes, Dryptini, Zuphiini, and Galeritini, all of which are circumtropical and partially temperate as well. One species of dryptine has been found in the Amazon Basin, the only member of the tribe in the New World. Both of the other two tribes have numerous species in the western hemisphere, including the West Indies.

### TRIBE ZUPHIINI

As delimited in Csiki (1932b:1562-1571), this is a very heterogeneous tribe. *Planetes* MacLeay belongs in the Galeritini; the Neotropical species of *Polystichus* Bonelli actually belong to a distinct genus, *Dailodontus* Reiche, which together with *Helluomorpha* Laporte has been removed to Helluonini (Reichardt, 1974b). *Pseudaptinus* Laporte, *Thalpius* LeConte, and *Mischocephalus* Chaudoir, have been transferred from "Dryptini" to Zuphiini (Reichardt, 1972b), and *Metaxidius* Chaudoir, placed traditionally among the Helluonini, actually belongs

Adult zuphiines are small-sized carabids, which apparently live in humus. Only Old World larvae are known.

Of the three known subtribes, only the Leleupidiina are not represented in the Neotropics. The tribe is worldwide in distribution, but is apparently predominant in the New World.

1	Maxillary palpomeres similar to labial palpomere . . . .	<i>Zuphiina</i> , <i>Zuphium</i> Latreille, p. 391	
1'	Maxillary palpomeres long and thick, with large terminal article; labial palpomeres short and thin, with small apical article . . . . .	<i>Patriziina</i> . . . . .	2
2 (1')	Pronotum without spine or sharp basal angles . . . . .	<i>Pseudaptinus</i> Laporte, p. 391	
2'	Pronotum with sharp basal angles . . . . .	<i>Thalpius</i> LeConte, p. 391	

This subtribe is composed of two genera with a total of 11 species known from the West Indies.

*Pseudaptinus* Laporte, 1835 (= *Diaphorus* Dejean). Exclusively American, with a few species in the United States, and a total of 16 Neotropical species. Liebke (1934:372-388) presented a key to the species (including *Thalpius*).

*Thalpius* LeConte, 1851 (= *Enaphorus* LeConte; = *Zuphiosoma* Laporte). Frequently considered a subgenus of *Pseudaptinus*, *Thalpius* has a disjunct distribution, with one Australian species (for which Laporte proposed the genus *Zuphiosoma*), and the remaining species in the New World, ranging from the southern United States to Argentina, including the West Indies.

*Zuphium* Latreille, 1806 (= *Zophium* Gistel; = *Zoyphium* Motschulsky). A genus with pantropical distribution, including Australia (56 species in the Old World, according to Csiki, 1932b:1562). In the New World, the genus ranges from the United States to Argentina, 20 Neotropical species being known of which only four are recorded from the West Indies. Identification of the species is difficult in spite of Liebke's key (1933:461-463). Mateu has studied the genus and revisions have started to appear (Mateu, 1981).

This is a moderately diverse, pantropical tribe. It was segregated from the Dryptini by Jeannel (1949:1057), but this action was not accepted by all recent authors (Darlington, 1971, uses Dryptini in the old sense).

The Western Hemisphere Galeritini were studied by Reichardt (1967). In this hemisphere, the tribe is predominantly Neotropical, only the subgenus *Progaleritina* occurring as far north as southern Canada. Eight species of *Galerita* are known from the West Indies.

Larvae of Neotropical forms (van Emden, 1942:51-52, 80) are very active, having been captured in forests, usually under leaves or stones. Reichardt (1971a) recorded "bombarding" habits in *Galerita corumbana* Liebke; the same habit was more recently observed in *Galerita collaris* Dejean. *Galerita occidentalis* (Olivier), however, does not show this habit.

Basilewsky (1963:23), considered the group as a subfamily, and arranged the species in two tribes. Both groups are represented in the Neotropics, but only *Galerita* has been found in the West Indies.

#### Key to Subgenera of West Indian Galeritini

- 1        Elytron with flat or evenly convex intervals . . . . . *Progaleritina* Jeannel
- 1'       Elytron with costate or multicarinate intervals . . . . . *Galerita* Fabricius

### SUPERTRIBE CTENODACTYLITAE

At present this supertribe includes the Old World Hexagoniini and the New World Ctenodactylini and Calophaeniini (Stork, pers. comm.), however the taxonomy is inadequate and needs complete revision on a worldwide basis. There are still parts of Odacanthini that belong here according to Stork (in litt.).

#### TRIBE CTENODACTYLINI

Delimitation of this small tribe of carabids has been relatively difficult, especially because of the confusion created by Liebke, who in a final revision of the group (1938) fused the Ctenodactylini and Odacanthini, as well as other groups which are actually unrelated (see also comments under Odacanthini and Lachnophorini).

Liebke (1928a and 1928b) revised this "subfamily", describing new genera and species. Later (1931), he presented a new key for identification of genera and descriptions of new genera and species. Finally, in the 1938 revision, the group was revised on a worldwide basis.

The tribe, as considered here, is predominantly Neotropical, but some genera may occur in the Old World, having been placed by Jeannel (1948:759) in the Hexagoniini.

Practically nothing is published about way of life of the Neotropical species, however, they are usually collected at lights and by sweeping emergent vegetation or stands of *Heliconia*-like broad leaf plants; adults are also semi-arboreal in low vegetation at the edge of water bodies. Larvae are known to pupate in the hollow culms of grasses. Van Emden (1942: 51) described the larva of *Leptotrachelus*.

Identification, even of genera, is presently difficult, and it is probable that many of Liebke's genera will not survive a careful study.

*Leptotrachelus* Latreille, 1829 (= *Rhagocrepis* Eschscholtz; = *Odacantha* Perty; = *Sphaeracra* Say). With 32 Neotropical species, of which only one is from the West Indies.

### SUPERTRIBE LEBIITAE

This supertribe approaches the pterostichites in size and diversity; however, recent studies by Ball (1975, 1983), Ball and Shpeley (1983), and Ball and Hilchie (1983) have begun to clear the complexities of earlier classifications. The arrangements of taxa presented here is



based on Erwin (1985) and is somewhat provisional, however all the groups included have highly developed bilateral turrets as a means of delivery for their chemical defence.

### TRIBE PERIGONINI

This is a tribe of very few species included in four genera (Csiki, 1931:894-899), of which three are Neotropical, and *Perigona* Laporte, 1835, which is worldwide in distribution, with nearly 80 species. Jeannel (1942a:577) considered the tribe as a subfamily of Perigonidae, together with Anchonoderinae, Omphreinae, and Lachnophorinae. Because of the structure of the defence mechanism, Erwin (1979, 1984) regarded this group as part of the Lebiitae.

Adults and larvae of *Perigona* live under bark of wet trees and in decaying leaf litter at low and middle altitudes. Many adults are attracted to fermenting sap and pulp of pithy tree species (especially certain palms). During dry season, adults of *Perigona* and *Diploharpus* are found in deep leaf piles beneath crowns of fallen trees. *Mizotrechus* members are found under deeply embedded stones in cloud forests at middle elevations and have been repeatedly taken in light traps in Panamá.

*Perigona* Laporte, 1835. Jeannel (1951) included the Neotropical species in *Perigona s. str.*, together with other species from the Old World tropics. Five species have been recorded from the West Indies.

### TRIBE LACHNOPHORINI

This is a weakly characterized group of still uncertain position and constitution and in some ways is linked to Agonini via genus *Anchonoderus*. However, Liebherr (1983) showed that female genitalia are more lebiine-like than agonine-like. Several of the lachnophorine genera were included in Colliurini by Liebke (1938). Jeannel (1942a:577) included Lachnophorini, together with Anchonoderini, both as subfamilies, in Perigonidae. Later (1948:742) he erected the family Lachnophoridae for the two subfamilies. For his Lachnophoritae, Jeannel erected two tribes, Lachnophorini and Selinini, based on misinterpretation of the terminal article of the maxillary palps, as discussed by Reichardt (1975).

Ball (1960:136, 137) considered Anchonoderini and Lachnophorini distinct tribes. Lindroth (1966:422) united Anchonoderini and Agonini, retaining them as a subtribe of Pterostichini, and considered Lachnophorini as a distinct tribe (Lindroth, 1969b:xxii). Whitehead & Ball (1975:595) considered Lachnophorina a subtribe of Pterostichini. Recently, Ball and Hilchie (1983) have concluded that the generic complex centered around *Eucaerus* belongs to this subtribe and this was substantiated by Liebherr (1983).

Immature stages of Neotropical species are unknown, however, Liebherr (1983) has amply described the larva of *Chalybe sallei*. Most species are riparian, living on river beaches, and others live in clearings in lowland and upland forests, including the red lateritic clays thrown up by leaf-cutter ants of the genus *Atta*. Adults seem to be good flyers and are frequently collected at light.

#### Key to Genera of West Indian Lachnophorini

- 1        Body densely pubescent or setiferous . . . . . 2
- 1'      Body glabrous (except for usual fixed setae) . . . *Eucaerus* LeConte, p. 394

- 2 (1) Maxillary palp with ultimate article nearly filiform, apically truncate . . .  
 . . . . . *Anchonoderus* Reiche, p. 394
- 2' Maxillary palp with ultimate article fusiform or ovoid and apically  
 subulate . . . . . 3
- 3 (2') Apical palpomeres fusiform; integument black; dorsal setae erect, sparse,  
 some as long as scape . . . . . *Euphorticus* Horn, p. 394
- 3' Apical palpomeres ovoid, apically subulate and pointed; integument pale;  
 dorsal surface densely pubescent with several thick and long black setae  
 sparsely arranged . . . . . *Lachnophorus* Dejean, p. 394

*Anchonoderus* Reiche, 1843. With 24 Neotropical species, of which only two are known from the West Indies. Its systematic position has also been discussed by a variety of authors.

*Lachnophorus* (*sensu lato*) Dejean, 1831 (= *Stigmaphorus* Motschulsky, 1862). Liebke (1936) recognized three subgenera, and presented keys to species. One species has been recorded from the West Indies.

*Euphorticus* Horn, 1881. The range of this genus extends from northwestern South America to southern United States. One species has been recorded from the West Indies.

*Eucaerus* LeConte, 1853. With 11 Neotropical species, of which eight are known from Brazil. One species occurs in southern United States. Two species have been described from the West Indies by Darlington.

#### TRIBE CYCLOSOMINI (=TETRAGONODERINI; MASOREINI *AUCT.*, in part)

The name Tetragonoderini is a junior synonym of Cyclosomini, recent usage to the contrary notwithstanding. This tribe is pantropical, and is most speciose in Africa and South America. This tribe and the Masoreini seem to be closely related, and Jeannel (1949) and Ball (1983) combined the two as a single group. Only one genus of Cyclosomini is known from the New World.

*Tetragonoderus* Dejean, 1829. (= *Peronoscelis* Chaudoir). This genus is pan-tropical, ranging in the New World from Chile to southeastern Ontario, in Canada. Adults live among dry leaves, on sand, along water courses. Many adults are taken at light, at night. Although only one species has been reported from the West Indies (Bahamas), at least two others occur in the Greater Antilles.

#### TRIBE MASOREINI (=ANALACINI)

Like the Cyclosomini, the limits of this pan-tropical tribe are not clear. Ball (1983) defines the problems that must be solved to clarify limits of the group and ranks of included taxa.

#### Key to Genera of West Indian Masoreini

- 1 Pronotum with base narrowed, sides markedly but evenly constricted  
 posteriorly. Microsculpture of elytron with meshes only slightly elongate,  
 nearly isodiametric, surface dull. . . . . *Aephnidius* MacLeay, p. 395
- 1' Pronotum with base wide, only slightly narrower than maximum width.  
 Elytron with microsculpture meshes elongate, surface  
 iridescent . . . . . *Macracanthus* Chaudoir, p. 395

*Macracanthus* Chaudoir, 1846a (= *Masoreus*, in part, *auct.*). The species of this endemic New World group seem to be related to those of the Old World genus *Anaulacus* MacLeay. In fact, these groups may be congeneric. Six species are known from the Neotropical Region, only one of which, *M. brevicillus* (Chevrolat) is known from the Greater Antilles.

*Aephnidius* MacLeay, 1825: 33 (= *Masoreus* in part, *auct.*). This is a pantropical group, comprising of 16 described species, of which two are known from the Neotropical Region. One of these, *A. ciliatus* Mutchler, occurs in the Greater Antilles, only.

### TRIBE PENTAGONICINI

This tribe is of cosmopolitan distribution, but with predominance in Asia, southeast Asian islands, and Australia-New Zealand. Two genera are endemic to Australia and New Zealand; *Scopodes* Erichson and *Actenonyx* White. All remaining species, including the Neotropical ones, are included in *Pentagonica* Schmidt-Goebel (= *Rhombodera* Reiche, *nec* Burmeister; = *Didetus* LeConte).

Liebke (1939a:129) described a monobasic genus, *Thoasia*, which he placed in Pentagonicini in spite of bilobed tarsomere 4 and pectinate claws (bilobed and smooth claws characterize pentagonicine adults). Reichardt (1968:147) maintained the genus in that tribe, but it seems now that its correct position is in Lebiini.

Reichardt (1968) published a preliminary revision of the New World species, of which 27 are recorded from the Neotropical Region, five from the West Indies.

Larvae and habits of *Pentagonica* members are unknown. Moore (1965:161-162, fig. 8-9) described the larva of *Scopodes simplex*. According to Moore, larval characteristics indicate relationship between Pentagonicini and Odacanthini.

### TRIBE ODACANTHINI (=COLLIURINI)

A tribe of small, predaceous carabids, usually found inhabiting forests and marshes, or river banks, and world-wide in distribution. Liebke (1930) revised the American species of the tribe and later (1938), the world fauna, however, including in it the Ctenodactylini (an action already made by Csiki, 1932b:1517-1547). Here more recent authors are followed, who consider the Odacanthini as distinct from Ctenodactylini. Van Emden (1942:51), who described Old World larvae, also united the two tribes in one.

Excluding Ctenodactylini, the tribe is of limited diversity, with a large cosmopolitan genus, *Colliuris* Degeer, and another 15 less diverse genera. Only three are known from the Neotropical Region, and the species of *Colliuris* are arranged in many subgenera.

*Colliuris* (*sensu lato*) Degeer, 1774 (= *Casnonia* Latreille & Dejean; = *Ophionea* Klug). A worldwide genus, with about 100 Neotropical species, seven of which occur in the West Indies. Adults of all species are small, winged, and most live in forests on vegetation, or in marshes. In two revisions, Liebke (1930, 1938) recognized many subgenera, most of which will probably have to be suppressed when they are better studied.

### TRIBE LEBIINI

This is a markedly diverse tribe, especially numerous in the tropics, with some genera, such as *Lebia*, *Agra*, and *Calleida*, with hundreds of species. About 60 genera with nearly 1,000

species are known already from the Neotropical Region; no doubt these are provisional numbers. Recent revisions show that the number of undescribed species is extensive.

Because of its diversity, the taxonomic state of the tribe in some areas is chaotic, especially because it has not been studied as a whole in the Neotropics. Even the suprageneric classification is not yet definitely established. Most groupings have been proposed for restricted faunas, e.g. for France (Jeannel, 1942a); Madagascar (Jeannel, 1949); Africa (Basilewsky, 1953); United States (Ball, 1960); Japan (Habu, 1967); and Canada (Lindroth, 1969a). Unfortunately there is no generally accepted system. The Neotropical genera deviate in certain characters, and do not fit easily into other systems. Many genera are monobasic, and have not been re-studied in recent years. Other genera, like those of the Calleidina, proposed by Liebke, are probably not natural, and are based on characters of difficult verification (mostly mouthparts).

Ball's recent revisions of the subtribe Pericalina (1975), "Euchelini" (and Shpeley, 1983), and Cymindina (and Hilchie, 1983), clearly show the previous chaotic state of the tribe. In Ball's sense, this subtribe includes groups such as the Mormolycini and other groups segregated by Jeannel.

It also seems better to include here, even though provisionally, the genus *Nemotarsus*, which has been variously placed in Masoreini by several authors, but has been returned to Lebiini by Ball (1960:157). The whole suprageneric system used here, however, is to be considered provisional. Many of the genera are placed in certain subtribes only because they have been placed there in catalogs (Csiki, 1932b). Their final position depend on future studies.

Patterns of life of members of Lebiini are most interesting, but little is known about the Neotropical representatives of the tribe. Adults are normally diurnal, brightly colored, frequently with metallic colors. Most members are small, but a few are relatively large (adults of *Agra* and *Chelonodema*, for example). Representatives of *Agra*, *Lebia*, and *Calleida* are planticolous, living on herbs, shrubs and trees, and even on flowers; *Lebia* species (adults and larvae) are frequently associated with species of Chrysomelidae. Larvae of species of *Lebia* are ectoparasitoids on pupae of Chrysomelidae. Larvae and adults of species of *Calleida* are predators, some specialized on caterpillars of Noctuidae and Pyralidae. *Cyminidis* and some *Apenes* adults are nocturnal, xerophytic species of sandy areas and sparse vegetation, and during the day, they hide under stones and under layers of vegetation. Van Emden (1942:47-51) described larvae of some genera, but very few from the Neotropical Region.

Key to Subtribes of West Indian Lebiini

- 1        Ventral surface of head behind mentum with one or more pairs of "suborbital" setigerous punctures, each seta about as long as supraorbital setae ..... 2
- 1'       Ventral surface of head without suborbital setae ..... 4
- 2 (1)   Antennomeres 5 to 11 each with ventral pit with many short sensory setae ..... Calleidina, *Euproctinus* Leng and Mutchler, p. 399
- 2'       Antennomeres without sensory pits ..... 3
- 3 (2')  Labrum elongate, at least as long as wide. Elytron with penultimate umbilical puncture closer to margin than those adjacent; apex obliquely truncate ..... Pericalina, p. 397
- 3'       Labrum transverse, wider than long. Elytron with penultimate umbilicate

- puncture same distance from margin as adjacent punctures; apex rounded ..... Lebiidiina, p. 398
- 4 (2') Elytron with three umbilicate punctures at outer apical angle in form of triangle ..... Lebiina, p. 399
- 4' Elytron with umbilicate punctures aligned linearly or nearly so ..... 5
- 5 (4') Tarsomere 4 bilobed ..... Calleidina, p. 398
- 5' Tarsomere 4 at most emarginate ..... 6
- 6 (5') Total length less than 6.0 mm ..... Dromiina, p. 397
- 6' Total length more than 6.0 mm ..... Apenina, p. 397

### SUBTRIBE APENINA

The subtribe was recently recognized by Ball (1983), and the genus-group taxa mostly at the generic level were revised by Ball and Hilchie (1983). One genus is represented in the Neotropical Region.

*Apenes* (*sensu lato*) LeConte, 1852. A genus of extensive distribution in the Western Hemisphere, but predominantly Neotropical where 60 species are known, with 14 of these occurring in the West Indies.

### SUBTRIBE DROMIINA

The genera which constitute this subtribe are better represented in temperate than tropical zones. In the Neotropical Region, they are in México, Central America, the West Indies, and Chile. The classification is not well understood and there are only revisions of a few genera.

#### Key to Genera of West Indian Dromiina

- 1 Base of pronotum broadly lobed ..... *Microlestes* Schmidt-Goebel, p. 397
- 1' Base of pronotum truncate ..... *Apristus* Chaudoir, p. 397

*Apristus* Chaudoir, 1846b. A cosmopolitan genus, with five Middle American species and one from the West Indies.

*Microlestes* Schmidt-Goebel, 1846 (= *Blechrus* Motschulsky; = *Bomius* LeConte; = *Dromius* Sloane). A cosmopolitan genus, with many Nearctic species, but few in the Neotropics. Mateu (1974) studied the five Mexican species, some of which also occur in the United States; one species is also known from Cuba.

### SUBTRIBE PERICALINA (=COPTODERINA, =CATASCOPIA, =THYREOPTERINA; INCLUDING MORMOLYCINI)

According to Ball (1975) in his revision of the subtribe, Pericalina includes some genera of previously uncertain position (like *Mormolyce* Hagenbach, in the past considered a distinct subfamily or tribe) and other genera previously distributed in different subtribes of Lebiini (or even other tribes, like Agonina or Pterostichini).

The Neotropical species are included mostly in endemic genera, some with a few species which range into southern United States. *Catascopus* and *Coptodera* are worldwide genera, with a few Neotropical representatives.



Key to Genera of West Indian *Calleidina*

- 1 Head with one pair of suborbital setigerous punctures. Mentum without tooth ..... *Euproctinus* Leng & Mutchler, p. 399
- 1' Head without suborbital setigerous punctures. Mentum with tooth ..... 2
- 2 (1') Ligula with four apical setae. Tarsomere 4 deeply emarginate, but not bilobed ..... *Plochionus* Latreille & Dejean, p. 399
- 2' Ligula with two apical setae ..... *Calleida* Dejean, p. 399

*Calleida* Dejean, 1825 (= *Callida* auct.). A markedly diverse, cosmopolitan genus, with 171 Neotropical species, of which six are recorded from the West Indies. Chaudoir (1872b) revised the species known at the time, but many were described later, especially by Liebke. Some authors consider *Spongoloba* Chaudoir, 1872b congeneric with *Calleida*; others (Lindroth, 1969a:1058) consider it a subgenus, apparently restricted to Nearctic species. *Philophuga* Motschulsky, has also been considered a distinct genus, for two Nearctic species of México, but Lindroth (1969a) considers it a subgenus of *Calleida*.

*Euproctinus* Leng & Mutchler, 1927 (= *Euproctus* Solier, nec Gene; = *Andrewesella* Csiki). A Neotropical genus which ranges into United States. There are 17 Neotropical species, of which one has been recorded from the West Indies. This group should probably be placed in a separate subtribe.

*Plochionus* (*sensu lato*) Latreille & Dejean, 1824. With few species, mainly restricted to the Western Hemisphere, including two species from the West Indies.

## SUBTRIBE LEBIINA

In number of species this is the most diverse subtribe (about 500), more than 450 in the cosmopolitan genus *Lebia* (*sensu lato*) alone. Chaudoir (1870, 1871a) monographed the group, arranging the species in several genera which are usually accepted by the "French school". In a study of the Nearctic fauna, however, Madge (1967) placed most of Chaudoir's generic names in synonymy. This concept has been accepted in more recent years, e.g. by Lindroth (1969a) and Reichardt (1972a).

The taxonomic position of the South American "genera" thus depends on further studies.

*Cryptobatis*, *Alkestis*, *Hyboptera* and *Aspasiola* have been placed in Physoderina by Csiki (1932b:1946). Jeannel (1949:882) restructured the groups, and restricted Physoderina to Indo-Malayan species. It seems, however, that *Cryptobatis* and *Hyboptera* are true Lebiina; *Alkestis* and *Aspasiola* are inadequately known genera, but should probably be placed here as well.

*Lebia* Latreille, 1802. Probably one of the largest genera of Carabidae, is of worldwide distribution, as has been seen above, and is also very numerous in the Neotropics. Only five species have been recorded in the West Indies, but surely this is from lack of collecting in their habitat or lack of study of collected material.

## ACKNOWLEDGEMENTS

We greatly appreciate suggestions made by various of the revisors listed in Appendix B, and we thank the following people who helped us put together this paper: George L. Venable, for the drawings of *Bembidion darlingtoni* and map; Dora V. Rios for translating the abstract into

Spanish.

# LITERATURE CITED

- Allen, R. T. 1972. A revision of the genus *Loxandrus* (Coleoptera: Carabidae) in North America. *Entomologica Americana*, 46: 1-184.
- Allen, R. T. and G.E. Ball. 1980. Synopsis of Mexican taxa of the *Loxandrus* Series (Coleoptera: Carabidae: Pterostichini). *Transactions of the American Entomological Society* 105: 481-576.
- Alluaud, C. 1919. Contributions á l'étude des Carabiques d'Afrique et de Madagascar (Col.) XXIII. Observations sur divers Clivinides: descriptions d'une race, d'une espèce et d'un genre nouveaux. *Bulletin de la Société Entomologique de France*, 5: 97-102.
- Alluaud, C. 1933. Étude des *Tachys* du sous-genre *Trepanotachys* Alluaud. *AFRA cahiers D'entomologie*, 7: 17-20.
- Apfelbeck, V. 1918. Koeopteren aus den nordalbanischmontenegrinischen Grenzgebiete. *Sitzungsberichte der Akademie der Wissenschaften in Wien, Abt. 1*, 127: 159-176.
- Arrow, C.J. 1942. The Beetle Family Rhysodidae, with some new species and a key to those at present known. *Proceedings of the Royal Entomological Society of London (B)*, 11: 171-183.
- Ball, G. E. 1959. A taxonomic study of the North American Licinini with notes on the Old World species of the genus *Diplocheila* Brullé (Coleoptera). *Memoirs of the American Entomological Society*, 16: 1-258.
- Ball, G. E. 1960. Carabidae (Latreille, 1810). In, Arnett, R. H. *The Beetles of the United States*. The Catholic University of American Press, Washington, D.C. pp. 55-181.
- Ball, G. E. 1965. Two new subgenera of *Pterostichus* Bonelli from western United States, with notes on characteristics and relationships of the subgenera *Paraferonia* Casey and *Feronia* Casey (Coleoptera: Carabidae). *Coleopterists Bulletin*, 19: 104-112.
- Ball, G. E. 1975. Percaline Lebiini: Notes on classification, a synopsis of the New World genera, and a revision of the genus *Ploeoxena* Chaudoir (Coleoptera: Carabidae), *Quaestiones Entomologicae*, 11: 143-242.
- Ball, G. E. 1983. Evaluation of the Baron Maximilien de Chaudoir's contribution to classification of cymindine Lebiini and Masoreimorphi (Coleoptera: Carabidae). *Coleopterists Bulletin*, 36: 513-530.
- Ball, G. E. and G. Hilchie. 1983. Cymindine Lebiini of Authors: definition and reclassification of Genera (Coleoptera: Carabidae). *Quaestiones Entomologicae*, 19: 83-216.
- Ball, G. E. and R. E. Roughley. 1982. The *Hypherpes* - like taxa of southern Mexico: Classification and evolutionary considerations (Coleoptera: Carabidae: (*Pterostichus*)). *Transactions of the American Entomological Society*, 108: 315-399.
- Ball, G. E. and D. Shpeley. 1983. The species of Eucheiloid Pericalina: Classification and evolutionary considerations (Coleoptera: Carabidae: Lebiidini). *Canadian Entomologist*, 115: 743-806.
- Bänninger, M. 1921. Vierter Beitrag zur Kenntnis der Carabinae. (Col.). *Gattung Omophron*. *Entomologische Mitteilungen*, 10: 112-120.
- Bänninger, M. 1927. Die Ozaenini (Col., Carab.). 10. Beitrag zur Kenntnis der Carabinae. *Deutsche Entomologische Zeitschrift*, 3: 177-216.
- Bänninger, M. 1935. Über alte und neue Formen der Subtr. Scaritini (Carab.).



- Entomologische Blätter, 31: 148–160.
- Bänninger, M. 1937. Über sudamerikanische *Taeniolobus*-Arten (Col. Carab.). *Ibid.*, 33: 320–322.
- Bänninger, M. 1938. Monographie der Subtribus Scaritina (Col. Carab.) II. Deutsche Entomologische Zeitschrift, 1938, pp. 41–181.
- Bänninger, M. 1939. Monographie der Subtribus Scaritina (Col. Carab.) III. *Ibid.*, I-IV: 136–161.
- Bänninger, M. 1949. Über Carabinae (Col.) Ergänzungen und Berichtigungen III, mit Bemerkungen zu R. Jeannel's neuer Einteilung der Carabiden. Mitteilungen der Münchener Entomologische Gesellschaft (e.v.), 39: 127–157.
- Barr, T. C., Jr. 1965. A new cavernicolous sphodrine from Veracruz, Mexico (Coleoptera: Carabidae). *Coleopterists Bulletin*, 19: 65–72.
- Barr, T. C., Jr. 1970. Studies of the Mexican subgenus *Platynella* Casey (Coleoptera: Carabidae: Agonini). *Psyche*, 77: 209–216.
- Barr, T. C., Jr. 1973. *Specocolpodes*, a new genus of troglolbitic beetles from Guatemala (Coleoptera: Carabidae). *Ibid.*, 80: 271–276.
- Basilewsky, P. 1953. Carabidae (Coleoptera: Adephaga). Exploration du Parc National de l'Upemba, 10: 1–252.
- Basilewsky, P. 1962. Les Ozaeninae d'Afrique et de Madagascar (Coleoptera, Carabidae). *Revue de Zoologie et Botanique Africaine*, 66: 291–314.
- Basilewsky, P. 1963. Révision des Galeritininae d'Afrique et de Madagascar. (Coleoptera: Carabidae). *Annales, Musée Royal de l'Afrique Centrale*, No. 120, 93 pp.
- Basilewsky, P. 1966. Révision des *Megacephala* d'Afrique (Coleoptera: Carabidae Cicindelinae). *Ibid.*, 152: 1–149.
- Basilewsky, P. 1972. La fauna terrestre de l'Ile de Sainte-Hélène. II. Insectes, Part 9. Coleoptera I. Fam. Carabidae. *Ibid.*, 192: 11–84.
- Bates, W. H. 1871a. Notes on Carabidae, and descriptions of new species (No. 5). *Entomologists' Monthly Magazine*, 8: 29–34.
- Bates, W. H. 1871b. Notes on Carabidae, and descriptions of new species (No. 2). *Ibid.*, 7: 244–248.
- Bates, W. H. 1872a. Notes on Carabidae, and descriptions of new species (No. 12). *Ibid.*, 8: 199–202.
- Bates, W. H. 1872b. Notes on Cicindelidae and Carabidae and descriptions of new species (No. 14). *Ibid.*, 8: 263–266.
- Bates, W. H. 1873. On the geodephagous Coleoptera of Japan. *Transaction of the Entomological Society of London*, 1873, pp. 219–322.
- Bates, W. H. 1878. On new genera and species of geodephagous Coleoptera from Central America. *Proceedings of the Zoological Society of London*, 1878, pp. 587–609.
- Bates, W. H. 1882. *Biologia Centrali-Americana*, Insecta, Coleoptera, Carabidae, vol. 1, pt. 1, pp. 40–152, pls. iii–v.
- Bates, W. H. 1883. *Ibid.*, Carabidae, Cicindelidae suppl., vol. 1, pt. 1, pp. 153–256, pls. vi–xii.
- Bates, W. H. 1884. *Ibid.*, vol. 1, pt. 1, pp. 257–299, pl. xiii.
- Bedel, L. 1879. Faune des coléoptères du bassin de la Seine. *Annales de la Société Entomologique de France*, volume hors series, 1: 1–128.
- Bedel, L. 1896. Catalogue raisonne des coléoptères du Nord de l'Afrique (Maroc, Algerie, Tunisie et Tripolitaine) avec notes sur la faune des Iles Canarie et de Madere. Paris. pp.

49–120.

- Bedel, L. 1902. Catalogue raisonné des coléoptères du Nord de d'Afrique (Maroc, Algérie, Tunisie et Tripolitaine) avec notes sur la faune des Iles Canarie et de Madère. Paris. pp. 201–264.
- Bell, R. T. 1960. A revision of the genus *Chlaenius* Bonelli (Coleoptera, Carabidae) in North America. Miscellaneous Publications of the Entomological Society of America, 1(3): 97–171.
- Bell, R. T. . 1970. The Rhysodini of North America, Central America, and the West Indies (Coleoptera: Carabidae). *Ibid.*, 6(6): 189–324.
- Bell, R. T. and J. R. Bell. 1962. The taxonomic position of the Rhysodidae (Coleoptera). *Coleopterists Bulletin*, 16: 99–106.
- Bell, R. T. and J. R. Bell. 1978. Rhysodini of the World. Part I. A new classification of the tribe, and a synopsis of *Omoglymmius* subgenus *Nitiglymmius*, new subgenus (Coleoptera: Carabidae or Rhysodidae). *Quaestiones Entomologicae*, 14: 43–88.
- Bell, R. T. and J. R. Bell. 1979. Rhysodini of the World. Part II. Revisions of the smaller genera (Coleoptera: Carabidae or Rhysodidae). *Quaestiones Entomologicae*, 15: 377–446.
- Benschoter, C. and E. Cook. 1956. A revision of the genus *Omophron* (Carabidae, Coleoptera) of North America north of Mexico. *Annals of the Entomological Society of America*, 49: 411–429.
- Bertkau, P. 1878. Bericht über die wissenschaftlichen Leistungen im Gebiete der Arthropoden während der Jahre 1877–78. *Archiv für Naturgeschichte* 44(1,Band 2): 219–562.
- Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part I. *Bulletin of the United States National Museum*, 185: 1–188.
- Boheman, C. H. 1958. Coleoptera. Species novas descripsit. In, *Kongliga Svenska Fregatten Eugenies resa omkring Jorden ... zoologi*, I. Insecta, pp. 1–112.
- Bonelli, F. A. 1810. Observations entomologiques (Caraben.) I. *Memorie della Reale-Accademia della Scienze di Torino*, 18: 21–78, (Synoptic table).
- Bonelli, F. A. 1813. Observations entomologiques (Caraben.) II. *Ibid.*, 20: 433–484.
- Böving, A. G. 1929. On the classification of beetles according to larval characters. *Bulletin of the Brooklyn Entomological Society*, 24: 55–80.
- Breuning, S. 1927. Monographie der Gattung *Calosoma* Web. (Carab.). *Koleopterologische Rundschau*, 13: 129–232.
- Breuning, S. 1928a. Monographie der Gattung *Calosoma* Web. (Carab.). *Weiner Entomologische Zeitung*, 44: 81–141.
- Breuning, S. 1928b. Monographie der Gattung *Calosoma* Web. *Koleopterologische Rundschau*, 14: 43–101.
- Brullé, G. A. 1834a. Histoire naturelle des insectes, vol. 4, Coléoptères I, 479 pp. Paris.
- Brullé, G. A. 1834b. Observations critiques sur la synonymie des Carabiques. *Revue d'Entomologie*, 2: 89–114.
- Brullé, G. A. 1835a. Observations critiques sur la synonymie des Carabiques. *Ibid.*, 3: 271–303.
- Brullé, G. A. 1835b. Leur classification et la description des espèces. In, Audouin, J. V. *Histoire naturelle des insectes*, Paris, vol. 5, Coléoptères II. 436 pp.
- Brullé, G. A. 1838. Insectes de l'Amérique méridionale recueillis par Alcide d'Orbigny. In, *Voyage dans l'Amérique méridionale ... par Alcide d'Orbigny*. Paris. vol. 2, pt. 2, pp. 17–56.
- Bruneau de Miré, B. 1952. Contribution a l'étude des Dyschiriinae (Col. Carabique) du Sahara

- Meridional et de ses confins Sahéliens. *Annales de la Société Entomologique de France*, 121: 49–116.
- Burakowski, B. 1975. Descriptions of larva and pupa of *Rhysodes sulcatus* (F.). (Coleoptera, Rhysodidae) and notes on the bionomy of this species. *Annales Zoologici*, 32: 271–387.
- Burmeister, M. H. 1841. Observations sûr les affinités naturelles de la famille des Pausidae [sic]. *Magazin de Zoologie*, No. 75, 15 pp., 76 pl.
- Carvalho, E. L. de 1959. Remarques sûr les *Paussus* du groupe *lineatus* et description d'une espèce nouvelle. *Revue Zoologique et Botanique Africaine*, 60: 17–20.
- Casey, T. L. 1884a. Contributions to the descriptive and systematic coleopterology of North America, part I, 60 pp., illus.
- Casey, T. L. 1884b. *Ibid.*, part II, pp. 61–198.
- Casey, T. L. 1897. Coleopterological notices. VII. *Annals of the New York Academy of Sciences*, 9: 285–684.
- Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America. *Memoirs on the Coleoptera*, 4: 1–192.
- Casey, T. L. 1914a. Some observations on the Carabidae, including a new subfamily. *Ibid.*, 5: 25–44.
- Casey, T. L. 1914b. A revision of the nearctic Harpalinae. *Ibid.*, 5: 45–305.
- Casey, T. L. 1918a. A review of the North American Bembidiinae. *Ibid.*, 8: 1–223.
- Casey, T. L. 1918b. Studies among some of the American Amarinae and Pterostichinae. *Ibid.*, 8: 224–393.
- Casey, T. L. 1920a. A revisional study of the American Platyninae. *Ibid.*, 9: 1–132.
- Casey, T. L. 1920b. Random studies among the American Caraboidea. *Ibid.*, 9: 133–299.
- Casey, T. L. 1924. Additions to the known Coleoptera of North America. *Ibid.*, 11: 1–347.
- Chaudoir, M. de. 1835. Description de quelques genres et espèces de Carabiques nouveaux. *Annales de la Société entomologique de France*, 4: 429–448.
- Chaudoir, M. de. 1838. Tableau d'une nouvelle subdivision du genre *Feronia* Dejean suivi d'une caractéristique de trois nouveaux genres de carabiques. *Ibid.*, 11: 3–32.
- Chaudoir, M. de. 1842. Description de quelques genres nouveaux de la famille des carabiques. *Ibid.*, 15: 832–857.
- Chaudoir, M. de. 1843. Carabiques nouveaux. *Ibid.*, 16: 671–695.
- Chaudoir, M. de. 1844. Trois memoires sûr la famille des carabiques. *Ibid.*, 17: 415–479.
- Chaudoir, M. de. 1846a. Note sur le groupe des Stomides et description d'un nouveau genre de celui des Somoplatides. *Ibid.*, 19: 511–542.
- Chaudoir, M. de. 1946b. Enumeration des Carabiques et des Hydrocanthares recueillis pendant un voyage au Caucase et dans les provinces transcaucasiennes par MM. de Chaudoir et le Baron A. de Gotsch, 269 pp. Kiew.
- Chaudoir, M. de. 1848. Mémoire sur la famille des carabiques. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 21: 3–134 (1. partie).
- Chaudoir, M. de. 1850a. Mémoire sur la famille des carabiques. *Ibid.*, 23: 3–85 (2<sup>e</sup>. partie).
- Chaudoir, M. de. 1850b. Mémoire sur la famille des carabiques. *Ibid.*, 23: 349–360 (2<sup>e</sup>. partie, cont.).
- Chaudoir, M. de. 1852. Mémoire sur la famille des carabiques. *Ibid.*, 25: 3–104 (3<sup>e</sup>. partie).
- Chaudoir, M. de. 1854. Mémoire sur la famille des carabiques. *Ibid.*, 27: 112–144 (4<sup>e</sup>. partie).
- Chaudoir, M. de. 1855. Mémoire sur les carabiques. *Ibid.*, 28: 1–110 (5<sup>e</sup>. partie).
- Chaudoir, M. de. 1856. Mémoire sur la famille des carabiques. *Ibid.*, 29: 187–291. (6<sup>e</sup>. partie).

- Chaudoir, M. de. 1857. Mémoire sur la famille des carabiques. *Ibid.*, 30: 1–64. (6<sup>e</sup>. partie, cont.).
- Chaudoir, M. de. 1859a. Beitrag zur Kenntniss der europäischen Feroniden. *Entomologische Zeitung, Stettin*, 20: 113–131.
- Chaudoir, M. de. 1859b. Monographie du genre *Colpodes* MacLeay. *Annales de la Société entomologique de France* (ser. 3), 7: 287–364.
- Chaudoir, M. de. 1861. Matériaux pour servir a l'étude des Cicindéletes et des Carabiques. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 34: 491–576.
- Chaudoir, M. de. 1862. Matériaux pour servir a l'étude des Cicindéletes et des Carabiques. *Ibid.*, 35: 275–320 (3<sup>e</sup>. partie).
- Chaudoir, M. de. 1965. Catalogue de la collection de Cicindéletes de M. le baron Chaudoir, 64 pp. Bruxelles.
- Chaudoir, M. de. 1868a. Note monographique sur le genre *Omophron*. *Revue et Magazin de Zoologie*, 20: 54–63.
- Chaudoir, M. de. 1868b. Observations synonymiques sur les carabiques de l'Amérique septentrionale et descriptions d'espèces nouvelles de ce pays. *Ibid.*, 20: 211–217, 239–245, 331–345.
- Chaudoir, M. de. 1869. Mémoire sur les thyroptérides. *Annales de la Société entomologique de Belgique*, 12: 113–162.
- Chaudoir, M. de. 1870. Monographie des lebiides. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 43: 111–231.
- Chaudoir, M. de. 1871a. Monographie des lebiides. *Ibid.*, 44: 1–87.
- Chaudoir, M. de. 1871b. Essai monographique sur le groupe des Pogonides. *Annales de la Société entomologique de Belgique*, 14: 21–61.
- Chaudoir, M. de. 1871c. Essai monographique sur les Orthogoniens. *Ibid.*, 14: 95–130.
- Chaudoir, M. de. 1872a. Observations sur quelques genres de carabiques, avec la description d'espèce nouvelles. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 45: 382–420.
- Chaudoir, M. de. 1872b. Monographie des callidides. *Annales de la Société entomologique de Belgique*, 15: 97–204.
- Chaudoir, M. de. 1874. Matériaux pour servir a l'étude des féroniens. *Bulletin de la Société Impériale des Naturalistes du Moscou*, 48: 1–34.
- Chaudoir, M. de. 1876a. Monographie des chleniens. *Annali del Museo Civico di Storia Naturale di Genova*, 8: 1–315.
- Chaudoir, M. de. 1876b. Étude monographique des Masoreides, des Tetragonoderides et du genre *Nematotarsus*. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 51: 1–84.
- Chaudoir, M. de. 1877. Genres nouveaux et espèces inédites de la famille des carabiques. *Ibid.*, 52: 188–268.
- Chaudoir, M. de. 1878a. Descriptions de genres nouveaux et d'espèces inédites de la famille des carabiques. *Ibid.*, 53: 1–80.
- Chaudoir, M. de. 1878b. Révision des genres *Onychopterygia*., *Dicranoncus* et *Colpodes*. *Annales de la Société entomologique de France* (ser. 3), 8: 275–382.
- Chaudoir, M. de. 1879. Monographie des Scaritides (Scaritini). *Annales de la Société Entomologique de Belgique*, 22: 124–182.
- Chaudoir, M. de. 1882a. Monographie des Oodides. *Annales de la Société entomologique de France* (ser. 4), 2: 317–378 (1, partie).

- Chaudoir, M. de. 1882b. Monographie des Oodides. *Ibid.*, 2:485–554 (2<sup>e</sup>. partie).
- Chevrolat, L. A. A. 1834a. Description de deux Megacephales. Revue d'Entomologie, publiée par G. Silberman. 2: 83–84.
- Chevrolat, L. A. A. 1834b. Coléoptères du Mexique, fasc. 2, [44 pp.]; fasc. 3, [49 pp.]; fasc. 4, [70 pp.]. Strasbourg.
- Chevrolat, L. A. A. 1835. Coléoptères du Mexique, fasc. 8, pp. 171–200. Strasbourg.
- Chevrolat, L. A. A. 1836. Description d'un *Carabus* de Porto-Ricco [sic]. Magasin de Zoologie, 6, pl. 169.
- Chevrolat, L. A. A. 1844. In, Guérin-Ménéville, F. E. Iconographie du règne animal de G. Cuvier, ou representation d'après nature de l'une espèces les plus remarquables et souvent non figurees de chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d'atlas à tous les traites de zoologie Fain and Thunot. Paris. vol. 3. Insectes. 576 pp.
- Chevrolat, L. A. A. 1858. Descriptions de coléoptères de la partie meridionale de l'Ile de Cuba. Revue et Magasin de Zoologie (ser. 2), 10: 209–212.
- Chevrolat, L. A. A. 1863. Coléoptères de l'Ile de Cuba. (Suite) Notes, synonymies et descriptions d'espèces nouvelles. Familles des cicindéletes, carabiques, dytiscides, gyrinides et palpicornes. Annales de la Société entomologique de France (ser. 4), 3: 183–210.
- Chevrolat, L. A. A. 1873. Descriptions de rhysodides nouveaux et enumeration des espèces decrits. *Ibid.*, (ser. 5), 3: 207–218.
- Chu, Hung-fu. 1945. The larvae of the Harpalinae Unisetosae (Coleoptera: Carabidae). Entomologica Americana, 25: 1–71.
- Crowson, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd and Co., London, 187 p.
- Crowson, R. A. 1967. Reprint of "The natural classification of the families of Coleoptera". E. W. Classey, London, 187 p.
- Crowson, R. A. 1981. The Biology of the Coleoptera. Academic Press, New York, 802 pp.
- Csiki, E. 1906. Magyarorszag Bogarfaunaja I, pp. 2.
- Csiki, E. 1928. Coleopterorum catalogus, pars 97, Carabidae: Mormolycinae & Harpalinae I., pp. 1–226.
- Csiki, E. 1929. Coleopterorum catalogus, pars 104, Carabidae: Harpalinae III, pp. 347–527.
- Csiki, E. 1930. Coleopterorum catalogus, pars 112, Carabidae: Harpalinae IV, pp. 529–737.
- Csiki, E. 1931. Coleopterorum catalogus, pars 115, Carabidae: Harpalinae V, pp. 739–1022.
- Csiki, E. 1932a. Coleopterorum catalogus, pars 124, Carabidae: Harpalinae VI, pp. 1023–1278.
- Csiki, E. 1932b. Coleopterorum catalogus, pars 124, Carabidae: Harpalinae VII, pp. 1279–1598.
- Darlington, P. J., Jr. 1933. A new tribe of Carabidae (Coleoptera) from Western United States. Pan-Pacific Entomologist, 9: 110–114.
- Darlington, P. J., Jr. 1934. New West Indian Carabidae, with a list of the Cuban species. Psyche, 41: 66–131.
- Darlington, P. J., Jr. 1935a. Three West Indian Carabidae in Florida. *Ibid.*, 42: 161–162.
- Darlington, P. J., Jr. 1935b. West Indian Carabidae II. Itinerary of 1934; forests of Haiti, new species; and a new key to *Colpodes*. *Ibid.*, 42: 167–215.
- Darlington, P. J., Jr. 1936. The species of *Stenomorphus* (Coleoptera: Carabidae), with data on heterogony in *S. californicus* (Mén). Pan-Pacific Entomologist, 12: 33–44.

- Darlington, P. J., Jr. 1937a. West Indian Carabidae III; new species and records from Cuba, with a brief discussion of the mountain fauna. *Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey"*, 11: 115–136.
- Darlington, P. J., Jr. 1937b. West Indian Carabidae IV. Three new *Colpodes*. *Psyche*, 44:122–124.
- Darlington, P. J., Jr. 1939. West Indian Carabidae. V. New forms from the Dominican Republic and Puerto Rico. *Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey"*, 13: 79–101.
- Darlington, P. J., Jr. 1941. West Indian Carabidae. VI. The Jamaican species, and their wings. *Psyche*, 48: 10–15.
- Darlington, P. J., Jr. 1947. West Indian Carabidae (Col.). VII. The species of the Cayman Islands. *Entomologists Monthly Magazine*, 83: 209–211.
- Darlington, P. J., Jr. 1950. Paussid Beetles. *Transactions of the American Entomological Society*, 76: 47–142.
- Darlington, P. J., Jr. 1953. West Indian Carabidae (Coleoptera). The Bahama species. *American Museum Novitates*, No. 1650, 16 pp.
- Darlington, P. J., Jr. 1970. Carabidae on tropical islands, especially the West Indies. *Biotropica*, 2: 7–15.
- Darlington, P. J., Jr. 1971. The Carabid beetles of New Guinea. Part IV. General considerations: analysis and history of fauna; Taxonomic supplement. *Bulletin of the Museum of Comparative Zoology*, 142: 129–337.
- Degeer, C. 1774. *Mémoires pour servir a l'histoire des insectes*, vol. 4, 456 pp., 19 pls. Stockholm.
- Dejean, P. F. M. A. 1825. *Spécies général des coléoptères de la collection de M. le comte Dejean*, vol. 1, 463 pp. Paris
- Dejean, P. F. M. A. 1826. *Ibid.*, vol. 2, 501 pp. Paris.
- Dejean, P. F. M. A. 1828. *Ibid.*, vol. 3, 556 pp. Paris.
- Dejean, P. F. M. A. 1829. *Ibid.*, vol. 4, 520 pp. Paris.
- Dejean, P. F. M. A. 1831. *Ibid.*, vol. 5, 883 pp. Paris.
- Dejean, P. F. M. A. and J. B. A. Boisduval, 1829. *Iconographie et histoire naturelle des coléoptères d'Europe*, vol. 1, 400 pp., pls. 1–60. Paris.
- Dokhtouroff, W. S. 1882. *Spec. Cicindel.*, I, p. 73 [from JUNK].
- Dokhtouroff, W. S. 1883. Zur quelques cicindelides nouveaux ou peu connus. *Revue Mensuelle d'Entomologie pure et appliquée*, 1: 274–276.
- Ehlers, W. 1884. Descriptions of new blind bembidii. *Transactions of the American Entomological Society*, 11: 1–36.
- Eisner, T. 1958. The protective role of the spray mechanism of the bombardier beetle, *Brachynus ballistarius* Lec. *Journal of Insect Physiology*, 2: 215–220.
- Eisner, T., T. Jones, D. Aneshansley, W. Tschinkel, R. Silberglied, and J. Meinwald. 1977. Chemistry of defensive secretions of Bombardier Beetles (Brachinini, Metriini, Ozaenini, Paussini). *Ibid.*, 23: 1383–1386.
- Emden, F. I. van. 1942. A key to the genera of larval Carabidae (Col.). *Transactions of the Royal Entomological Society of London*, 92: 1–99.
- Emden, F. I. van. 1953a. The Harpalini genus *Anisotarsus* Dejean (Col. Carab.). *Annals and Magazine of Natural History*, 12: 513–547.
- Emden, F. I. van. 1953b. The larva of *Morion* and its systematic position (Coleoptera:

- Carabidae). Proceedings of the Hawaiian Entomological Society, 15: 51–54.
- Emden, F. I. van. 1958. New South American Carabidae (Coleoptera) with notes on described species. *Annals and Magazine of Natural History*, 13: 19–32.
- Erichson, W. F. 1837. *Die Käfer der Mark Brandenburg*, vol. 1, pt. 1, pp. 1–384. Berlin.
- Erichson, W. F. 1848. *Die Insekten in Schomburg's Reise in Guiana*, vol. 3, pp. 533–617. Leipzig.
- Erwin, T. L. 1967. Bombardier Beetles (Coleoptera: Carabidae) of North America: Part II. Biology and Behaviour of *Brachinus pallidus* Erwin in California. *Coleopterists Bulletin*, 21: 41–55.
- Erwin, T. L. 1970. A Reclassification of Bombardier Beetles and a Taxonomic Revision of the North and Middle American species (Carabidae: Brachinida). *Quaestiones Entomologicae*, 6: 4–215.
- Erwin, T. L. 1971a. Notes and corrections to a reclassification of Bombardier beetles (Carabidae, Brachinida). *Ibid.*, 7: 1–281.
- Erwin, T. L. 1971b. Fossil Tachyine Beetles from Mexican and Baltic amber with notes on a new synonymy of an extant group (Col., Carabidae). *Entomologica Scandinavica*, 2: 233–236.
- Erwin, T. L. 1972. Om biologien hos bombarderbiller (Col., Carabidae, Brachinidae). *Entomologiske Meddr.*, 40: 65–71.
- Erwin, T. L. 1973. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part I. A Revision of the Neotropical genus *Xystosomus* Schaum. *Smithsonian Contributions to Zoology*, No. 140, 39 pp.
- Erwin, T. L. 1974a. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini) Supplement A: Lectotype Designations for New World Species, Two new genera, and notes on generic concepts. *Proceedings of the Entomological Society of Washington*, 76: 123–155.
- Erwin, T. L. 1974b. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini, Part II: A Revision of the New World Australian genus *Pericompsus* LeConte. *Smithsonian Contributions to Zoology*, No. 162, 92 pp.
- Erwin, T. L. 1974c. The genus *Coptocarpus* Chaudoir of the Australian Region with notes on related African species (Coleoptera: Carabidae: Oodini). *Ibid.*, No. 184, 25 pp.
- Erwin, T. L. 1975. Studies of the Subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part III: Systematics, phylogeny, and zoogeography of the genus *Tachyta* Kirby. *Ibid.*, No. 208, 68 pp.
- Erwin, T. L. 1976. A case of homonymy in the Tachyina (Coleoptera: Carabidae: Bembidiini). *Coleopterists Bulletin*, 29: 94.
- Erwin, T. L. 1978a. Studies of the Subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Supplement C: Discovery of the sister group of *Mioptachys* Bates in the Amazon Basin -- *Inpa psydroides* a new genus and species. *Ibid.*, 32: 29–36.
- Erwin, T. L. 1978b. The larva of Neotropical *Enceladus gigas* Bonelli (Coleoptera: Carabidae: Siagoninae: Enceladini) with notes on the phylogeny and classification of some of the more primitive tribes of ground beetles. *Ibid.*, 32: 99–106.
- Erwin, T. L. 1979. Thoughts on the evolutionary history of ground beetles: Hypothesis generated from comparative faunal analysis of lowland forest sites in Temperate and Tropical regions. In, Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern eds, *Carabid Beetles: Their evolution, natural history, and classification*. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk, Publishers, The Hague, pp.

539–592.

- Erwin, T. L. 1981. A synopsis of the immature stage of Pseudomorphini (Coleoptera: Carabidae) with notes on tribal affinities and behaviour in relation to life with ants. *Coleopterists Bulletin*, 35: 53–68.
- Erwin, T. L. 1982. Small terrestrial ground beetles of Central America (Carabidae: Bembidiina and Anillina). *Proceedings of the California Academy of Sciences*, 42: 455–496.
- Erwin, T. L. 1984. Composition and origin of the Ground-Beetle Fauna of Sri Lanka (Coleoptera; Carabidae). *In*, Fernando, C. H., *Ecology and Biogeography of Sri Lanka*. Dr. W. Junk, The Hague. *In press*.
- Erwin, T. L. 1985. The Taxon Pulse: A General Pattern of Lineage Radiation and Extinction Among Carabid Beetles. Dr. W. Junk, The Hague. *In Press*.
- Erwin, T. L. and L. V. M. Erwin. 1976. Relationships of predaceous beetles to tropical forest and wood decay. The natural history of Neotropical *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) and its implications in the evolution of ectoparasitoidism. *Biotropica*, 8: 215–224.
- Erwin, T. L. and D. H. Kavanaugh. 1980. On the identity of *Bembidion puritanum* Hayward (Coleoptera: Carabidae: Bembidiini). *Coleopterists Bulletin*, 34: 241–242.
- Erwin, T. L. and D. H. Kavanaugh. 1981. Systematics and zoogeography of *Bembidion* Latreille: I. The *Carlhi* and *Erasum* groups of Western North America (Coleoptera: Carabidae: Bembidiini). *Entomologica Scandinavica*, Supplement, 15: 33–72.
- Erwin, T. L. and N. Stork. 1984. The Hiletini, an ancient and enigmatic tribe of Carabidae with a pantropical distribution (Coleoptera). *In Press*. *Systematic Entomology*.
- Eschscholtz, J. P. 1829. *Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Theirarten, wahrend des Flottsapitians von Kotzebue zweiter Teise um die Welt, auf der Russisch-Kaiserlichen Kriegsschlupp Predpriatie in den Jahren 1823-1826*. Erstes Heft, 17 pp., illus. Berlin.
- Fabricius, J. C. 1775. *Systema entomologiae*, 30 + 832 pp. Lipsiae.
- Fabricius, J. C. 1781. *Species insectorum*, vol. 1, 552 pp.; vol. 2, 517 pp. Kilonii.
- Fabricius, J. C. 1787. *Mantissa insectorum*, vol. 1, 348 pp.; vol. 2, 382 pp. Hafniae.
- Fabricius, J. C. 1792. *Entomologia systematica*, vol. 1, 330 + 538 pp. Hafniae.
- Fabricius, J. C. 1798. *Supplementum entomologiae systematicae*, 572 pp. Hafniae.
- Fabricius, J. C. 1801. *Systema eleutheratorum*, vol. 1, 506 pp.; vol. 2, 687 pp. Kiliae.
- Fairmaire, L. 1849. Description de quelques Coléoptères nouveaux d'Europe et de France. *Annales de la Société entomologique de France*, 6:419–427.
- Fairmaire, L. 1901. Description de Coléoptères nouveaux de Madagascar. *Bulletin de la Société entomologique de France*, 1901, pp. 94–97.
- Fischer von Waldheim, G. 1921. Lettre a Pander, contenant une notice sur un nouveau genre d'oiseaux et sur plusieurs nouveaux insects, 15 pp. Moucou.
- Fleutiaux, E., and A. Sallé. 1889. Liste des coléoptères de la Guadeloupe et descriptions d'espèces nouvelles. *Annales de la Société entomologique de France*, (ser. 6), 9: 351–484.
- Ganglbauer, L. 1892. *Die Käfer von Mitteleuropa. Die Käfer der osterreichisch-ungarischen Monarchie, Deutschlands, der Schweiz, sowie des franzosischen und italienischen Alpengebietes*, vol. 1, Familienreihe Caraboidea, 557 pp. Wien.
- Gehin, J. J. B. 1876. Catalogue synonymique et systematique des Coléoptères Carabiques de la tribu les Carabides. pp. 1–72.
- Gehin, J. J. B. 1881. Note sur le *Calosoma blaptoides* Putzeys. *Bulletin de la Société*



- entomologique de France, 1881, pp. 82–84.
- Gehin, J. J. B. 1885. Catalogue synonymique et systematique de coléoptères de la tribu Carabides. Remiremont. pp. 1–104.
- Gemminger, M., and E. von Harold. 1868. Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus, vol. 1, 424 pp. Monachii.
- Germar, E.F. 1824. Insectorum species novae aut minus cognitae, descriptionibus illustratae, pp. 624. Halae.
- Gidaspow, T. 1959. North American Caterpillar Hunters of the genera *Calosoma* and *Callisthenes* (Coleoptera: Carabidae). Bulletin of the American Musuem of Natural History, 110: 229–343.
- Gidaspow, T. 1963. The genus *Calosoma* in Central America, the Antilles, and South America (Coleoptera, Carabidae). *Ibid.*, 124: 279–313.
- Gistel, J. N. F. X. 1837. Systema insectorum, secundum classes, ordines, genera, species, cum characteribus, synonymis, annotationibus, locis et iconibus, vol. 1, Heft 1, xvi + 104 pp. Monachii.
- Gistel, J. N. F. X. 1838. Systema insectorum, secundum classes, ordines, genera, species, cum characteribus, synonymis, annotationibus, locis et iconibus, vol. 1, Heft 2, pp. 65–132. Bernae.
- Gory, H. L. 1833. Centurie de carabiques nouveaux. Annales de la Société entomologique de France, 2: 168–247.
- Gozis, M. des. 1882. Mémoire sur les pores setigeres prothoraciques dans la tribu des carnivores. Schriften der Entomologische Gesellschaft 6(Heft 6): 285–300.
- Grey, B. 1937. The Coleoptera of Washington: Carabidae-Agonini. University of Washington, thesis, Seattle, Washington, pp. 309–313.
- Gray, G. R. 1832. Notices of new genera and species. In, Griffith and Pidgeon, The animal kingdom arranged in conformity with its organization by the Baron Cuvier, vol. 14 (Insecta, vol. 1), 570 pp. London.
- Grundmann, E. 1955. Beitrag zur Kenntnis der Carabiden-Subfamilie Chlaeiinae (Coleoptera Carabidae). Mémoires de la Société entomologique de Belgique, 27: 276–288.
- Guérin-Ménéville, F. E. 1845. (Note zur quelques coléoptères trouvés dans la racine de squine (*Smilax chine*)). Bulletin de la Société entomologique de France, 1845, pp. xvi–xvii.
- Gundlach, D. J. 1893. Apuntes para La Fauna Puerto-Riquena. Anales de la Sociedad Espanola de Historia Natural, (series II), 22: 286–294.
- Gyllenhal, L. 1806. in, Schönherr, E. Synonymia insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet, vol. 1, pt. 1, 294 pp. Stockholm.
- Habu, A. 1967. Carabidae. Truncatipennes group. (Insecta: Coleoptera). Fauna Japonica, xiv + 318 pp. Tokyo.
- Harris, T. W. 1828. Contributions to entomology. New England Farmer, 7(4): 132.
- Hatch, M. 1933. Notes on Carabidae. Pan-Pacific Entomologist, 9(3): 117–121.
- Hatch, M. 1949a. Studies on the fauna of Pacific Northwest greenhouses (Isopoda, Coleoptera, Dermaptera, Orthoptera, Gastropoda). Journal of the New York Entomological Society, 27: 141–165.
- Hatch, M. 1949b. Studies on the Coleoptera of the Pacific Northwest III. Carabidae: Harpalinae. Bulletin of the Brooklyn Entomological Society, 44(3): 80–88.
- Hatch, M. 1950. Studies on the Coleoptera of the Pacific Northwest II. Carabidae: Bembidiini.

- Pac-Pacific Entomologist, 26(3): 97–106.
- Hatch, M. 1953. The Beetles of the Pacific Northwest. Part I. Introduction and Adephaga. University of Washington Press, Seattle, 340 p.
- Haury, C. 1880. Description d'un nouveau genre de coléoptères de la famille des carabides. Le Naturaliste, 2: 164–165.
- Hayward, R. 1900. A study of the species of *Tachys* of boreal America. Transactions of the American Entomological Society, 26: 191–238.
- Herbst, J. F. W. 1784. Kritisches Verzeichniss meiner Insecten-Sammlung. Archiv der Insectengeschichte, 5: 68–151.
- Hlavac, T. F. 1969. A review of the species of *Scarites* (*Antilliscaris*), (Coleoptera: Carabidae) with notes of their morphology and evolution. Psyche, 76(1): 1–17.
- Hlavac, T. F. 1975. The prothorax of Coleoptera: (except Bostrichiformia-Cucujiformia). Bulletin of the Museum of Comparative Zoology, 147: 137–183.
- Hope, F. W. 1838. The coleopterist's manual, part the second, containing the predaceous land and water beetles of Linneus and Fabricius, 168 pp., illus. London.
- Hope, F. W. 1845. On the entomology of China, with descriptions of the new species sent to England by Dr. Cantor from Chusan and Canton. Transactions of the Entomological Society of London, 4: 4–17.
- Horn, G. H. 1876. Revision of the species of *Chlaenius* of the United States. Transactions of the American Entomological Society, 5: 253–276.
- Horn, G. H. 1881. On the genera of Carabidae with special reference to the fauna of boreal America. *Ibid.*, 9: 91–196.
- Horn, W. 1903. List of the Cicindelidae of Mexico and on their relationship with the species of the United States. Journal of the New York Entomological Society, 11: 213–221.
- Horn, W. 1910. Genera insectorum, Coleoptera, fam. Carabidae: subfam. Cincindelinae, fasc. 82B, pp. 105–208.
- Horn, W. 1923. Zur Systematic, Geographie und Lebensweise der Cicindelinae (Col.). Zoologische Jahrbücher, Abtheilung für Systematik, 47: 309–330.
- Horn, W. 1926. Über neue und alte Cicindelinen der Welt. Entomologische Blätter, 22: 164–173.
- Horn, W. 1936. Über die erste australische *Prothyma*-Art sowie über die Fauna von Haiti. *Ibid.*, 32: 22–24.
- Hubenthal, W. 1911. Bemerkungen zu der Carabidengruppe Brachynini und Beschreibungen des *Pheropsophus ecuadoriensis* und *langenhami* n. sp. (Col.). Deutsche Entomologische Zeitschrift, 1911, pp. 547–552.
- Jacquelin du Val, P. N. C. 1856. Coleoptera. In, Sagra, Historie physique, politique et naturelle de l'île de Cuba. Animaux articles, insectes, pp. 1–136. Paris.
- Jacquelin du Val, P. N. C. 1857. Insectes. Ordre des coléoptères, Lin. In, Sagra, Historie, physique, politique et naturelle de l'île de Cuba. Animaux articles, insectes, vol. 7, pp. 137–328. Paris.
- Jaennicke, R. 1867. Beiträge zur Kenntniss der europäischen Bombyliden, Acroceriden, Scenopiniden, Thereviden und Asiliden. Berliner Entomologische Zeitschrift, 11: 61–100.
- Jeannel, R. 1932. Revision du Genre *Limnastis* (Coleoptera). Annals de la Société entomologique de France, Livre du Centenaire, pp. 167–187.
- Jeannel, R. 1937. Les Bembidiides endogés (Col. Carabidae). Monographie d'une lignée gondwanienne. Revue Française d'Entomologie, 3: 241–396.

- Jeannel, R. 1940. Les Calosomes. Mémoires du Muséum d'Histoire Naturelle, 13: 81–240.
- Jeannel, R. 1941. Faune de France. vol. 39. Coléoptères Carabiques. (Première Partie), LeChevalier and Sons publishers, Paris, pp. 1–571.
- Jeannel, R. 1942a. *Ibid.*, (Deuxième Partie), 40: 573–1173.
- Jeannel, R. 1942b. La Genèse des Faunes terrestres; éléments de biogéographie. Presses universitaires de France, Paris. 513 pp.
- Jeannel, R. 1946. Coléoptères Carabiques de la Région Malgache (Première Partie). Faune de l'Empire Française, 6:1–372.
- Jeannel, R. 1948. Coléoptères Carabiques de la Région Malgache (Deuxième Partie) *Ibid.*, 10: 373–765.
- Jeannel, R. 1949. Coléoptères Carabiques de la Région Malgache (Troisième Partie). *Ibid.*, 11: 767–1146.
- Jeannel, R. 1951. In, Grassé, P.-P. and R. Jeannel. Un carabique termitophile nouveau de l'Afrique tropicale. Revue Française d'Entomologie, 18: 137–149.
- Jeannel, R. 1962. Les Trechides de la Palaentartide Occidentale. Biologie de l'Amerique Australe., Étude de la Faune du Sol. 1: 529–655.
- Jeannel, R. 1963. Monographie des "Anillini", Bembidiides endogés. (Coleoptera: Trechidae). Mémoires du Muséum d'Histoire Naturelle, Serie A- Zoology, 28: 33–204.
- Jorge-Silva, M. E. and C. Costa. 1983. Larvae of Neotropical Coleoptera. V: Carabidae, Morionini, Papéis Avulsos do Departamento de Zoologia, 35: 1–10.
- Kirby, W. 1825. A description of some insects which appear to exemplify Mr. William S. MacLeay's doctrine of affinity and analogy. Transactions of the Linnean Society of London, 14: 93–110.
- Kirby, W. 1835. The characters of *Clinidium*, a new genus of insects in the order of Coleoptera, with a description of *Clinidium guildingii*. The Zoological Journal, 5: 6–9.
- Kirby, W. 1937. Insects. Coleoptera. In, Richardson, Fauna Boreali-Americana; or the zoology of the northern parts of British America ..., 249 pp. Norwich.
- Klug, J. C. F. 1821. Entomologiae Brasilianae specimen. Nova Acta Physico-Medica Academiae Caesareae-Leopoldino-Carolinae, naturae Curiosorum, 10(2): 277–324.
- Klug, J. C. F. 1829. Preis-Verzeichniss vorräthiger Insectendoubletten des Königl. zoologischen Museums der Universität, 18 pp. Berlin.
- Klug, J. C. F. 1834. Jahrbucher der Insectenkunde, mit besonderer Rücksicht auf die Sammlung im Königl. Museum zu Berlin, vol. 1, 296 pp., 2 pls, Berlin.
- Kolbe, H. J. 1895. Über die in Afrika gefundenen montanen und subalpinen Gattungen der mit *Calosoma* verwandten Coleoptera. Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin, 1895, pp. 50–69.
- Kolbe, H. J. 1927. Die Einstammigkeit der Paussiden und die primitiven Gattungen dieser myrmekophilen Coleopterengamilie. Zoologischer Anzeiger, 122: 205–218.
- Kolbe, H. J. 1930. Paussidenstudien, gegen Wasmann. Deutsche Entomologische Zeitschrift, pp. 16–24.
- Kryzhanovsky, O. 1976. Revised Classification of the Family Carabidae (English translation from Russian). Entomological Review, 1: 80–89.
- Kult, K. 1947. The third study to the knowledge of tribus Clivinini (Col., Carab.). Casopis Československé Společnosti Entomologické, 44: 26–37.
- Kult, K. 1950. New neotropical species of the group Ardistominina (Carabidae, Col.). Arthropoda, 1: 299–325.

- Kult, K. 1959. Review of the African species of the Old World genus *Clivina* Latr. (Col. Carabidae). *Revue de Zoologie et de Botanique Africaines*, 60: 172–225.
- Kult, K. 1961. Beitrag zur Kenntnis der Tachyiini aus Iran (Coleoptera, Carabidae). *Stuttg. Beitr. z. naturkunde* 57, Stuttgart, pp. 1–4.
- Lacordaire, J. T. 1854. *Genera des coléoptères . . .*, vol. 2 548 pp., illus. Paris. (Contenant des familles des paussides, staphyliniens, psélaphiens, scydménides, silphales, sphériens, trichoptérygiens, scaphidiles, histériens, phalacrides, nitidulaires, trogositaires, colydiens, rhyssodides, cucujipes, cryptophagies, lathridiens, mycétophagides, thorictides, dermestins, byrrhiens, géoryssins, parnides, hétérocerides.).
- Laferté-Sénéctère, F. T. de 1841. Description de dix carabiques nouveaux du Texas et d'une espèce nouvelle de buprestide de France. *Revue Zoologique*, 1841, pp. 31–51.
- Laferté-Sénéctère, F. T. de 1851. Révision de la tribu des patellimanes de Dejean, coléoptères pentamères de la famille des carabiques. *Annales de la Société entomologique de France* (ser. 2), 9: 209–294.
- Laporte, F. L. N. de C. 1932. Mémoire sur cinquante espèces nouvelles ou peu connus d'insectes. *Annales de la Société entomologique de France*, 1: 386–415.
- Laporte, F. L. N. de C. 1834a. Description de deux nouvelles mégacéphales. *Revue Entomologique*, 2: 83–84.
- Laporte, F. L. N. de C. 1834b. Observations sur la tribu des cicindéletes. *Ibid.*, 2: 27–39.
- Laporte, F. L. N. de C. 1934c. Études entomologiques, ou description d'insectes nouveaux, et observations sur la synonymie, pt. 1, fasc. 1, pp. 1–94. Paris.
- Laporte, F. L. N. de C. 1835. Études entomologiques, ou description d'insectes nouveaux, et observations sur la synonymie, pt. 1, pp. 95–159. Paris.
- Laporte, F. L. N. de C. 1840. Histoire naturelle des animaux articulés, vol. 1, 324 pp. Paris.
- Laporte, F. L. N. de C. 1867. Notes on Australian Coleoptera. *Transactions of the Royal Society of Victoria*, 8: 95–225.
- Lapouge, G. V. de. 1924. Calosomes nouveaux ou mal connus (Col. Carabidae). *Miscellanea Entomologica*, 28: 37–44.
- Lapouge, G. V. de. 1929a. Sous-tribu des Calosomina. *Ibid.*, 32: 1–15.
- Lapouge, G. V. de. 1929b. *Genera insectorum*, Coleoptera, fam. Carabidae: subfam. Carabinae I, fasc. 192A, pp. 1–153.
- Lapouge, G. V. de. 1930. *Ibid.*, II, fasc. 192A, pp. 155–291.
- Lapouge, G. V. de. 1931. *Ibid.*, III, fasc. 192B, pp. 293–580.
- Lapouge, G. V. de. 1932. *Ibid.*, IV, fasc. 192C, pp. 582–747.
- Latreille, P. A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes, vol. 3, 467 pp. Paris.
- Latreille, P. A. 1804. Histoire naturelle, générale et particulière des crustacés et des insectes, vol. 9, 416 pp. Paris.
- Latreille, P. A. 1806. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*, vol. 1, 302 pp. Paris.
- Latreille, P. A. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposés en familles, 444 pp. Paris.
- Latreille, P. A. 1817. [Insects]. In, Cuvier, Règne animal ... , vol. 3, 653 pp. Paris.
- Latreille, P. A. 1829. Les crustacés, les arachnides et les insectes, distribués en famille naturelles, ouvrage formant les tomes 4 et 5 de celui de M. le Baron Cuvier sur le Règne animal

- (deuxieme edition), vol. 1, 584 pp. Paris.
- Latreille, P. A. and P. F. M. A. Dejean. 1822. Histoire naturelle et iconographie des insectes coléoptères d'Europe, livr. 1, pp. 1–89, pls. 1–5. Paris.
- Latreille, P. A. and P. F. M. A. Dejean. 1823. Histoire naturelle et iconographie des insectes coléoptères d'Europe, livr. 2, pp. 91–134, pls. 6–10. Paris.
- Latreille, P. A. and P. F. M. A. Dejean. 1824. Histoire naturelle et iconographie des insectes coléoptères d'Europe, livr. 3, pp. 135–198, pls. 11–15. Paris.
- Leach, W. E. 1815. (Articles on entomology). *In*, Brewster, Edinburgh Encyclopaedia. Vol. 9. 81 pp. Edinburgh.
- LeConte, J. L. 1845. Descriptions of some new and interesting insects, inhabiting the United States. *Boston Journal of Natural History*, 5: 203–209.
- LeConte, J. L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. *Annals of the Lycaenun of Natural History of New York*, 4: 173–474.
- LeConte, J. L. 1851. Descriptions of new species of Coleoptera, from California. *Ibid.*, 5: 125–216.
- LeConte, J. L. 1852. Synopsis of the species of *Pterostichus* Bon. and allied genera inhabiting temperate North America. *Journal of the Academy of Natural Sciences of Philadelphia*, (ser. 2), 2: 225–256.
- LeConte, J. L. 1853. Notes on the classification of the Carabidae of the United States. *Transactions of the American Philosophical Society*, 10: 363–403.
- LeConte, J. L. 1854. Synopsis of the species of *Platynus* and allied genera, inhabiting the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7: 35–59.
- LeConte, J. L. 1857. Synopsis of the species of *Clivina* and allied genera inhabiting the United States. *Ibid.*, 9: 75–83.
- LeConte, J. L. 1861. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. *Smithsonian Miscellaneous Collections*, No. 136, pp. 1–208.
- LeConte, J. L. 1863. New species of North American Coleoptera. Prepared for the Smithsonian Institution. *Ibid.*, No. 167, pp. 1–86.
- LeConte, J. L. 1873. The Pterostichi of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1873, pp. 302–320.
- LeConte, J. L. 1878. Additional descriptions of new species. *In*, Schwarz, T. The Coleoptera of Florida. *Proceedings of the American Philosophical Society*, 17: 373–434.
- Leng, C. W. 1915. List of the Carabidae of Florida. *Bulletin of the American Museum of Natural History*, 34: 555–601.
- Leng, C. W. and A. D. Mutchler. 1914. A preliminary list of the Coleoptera of the West Indies as recorded to January 1, 1914. *Ibid.*, 33: 391–493.
- Leng, C. W. and A. D. Mutchler. 1916. Descriptive catalogue of West Indian Cicindelidae. *Ibid.*, 35: 681–698.
- Leng, C. W. and A. D. Mutchler. 1917. Supplement to preliminary list of the Coleoptera of the West Indies. *Ibid.*, 37: 191–220.
- Leng, C. W. and A. D. Mutchler. 1927. Supplement 191–1924 (inclusive) to catalogue of the Coleoptera of America, north of Mexico, 78 pp. Mount Vernon, N. Y.
- Lenko, K. 1972. *Pseudomorpha laevissima* um carabideo mirmecofilo (Coleoptera: Carabidae). *Studia Entomologia*, 15: 439–441.
- Liebke, M. 1928a. Laufkäfer Studien IV. *Entomologischer Anzeiger*, 8: 133–136, 151–152.

- Liebke, M. 1928b. Laufkäfer Studien V. *Ibid.*, 8: 174–177, 185–186, 189–193, 198–201, 205–209, 215–218, 221, 224.
- Liebke, M. 1930. Revision der amerikanischen Arten der Unterfamilie Colliurinae (Col. Carab.). Mitteilungen aus dem zoologischen Museum in Berlin, 15: 647–726.
- Liebke, M. 1931. Laufkäfer Studien VIII. Neue-Gattungen und Arten der Unterfamilie Ctenodactylinae. Entomologischer Anzeiger, 11: 358–361, 389–392.
- Liebke, M. 1933. Die amerikanischen Arten der Gattung *Zuphium* (Col. Carab.). Revista de Entomología, 3: 461–472.
- Liebke, M. 1934. Die Arten der Gattung *Pseudaptinus* Cat. (Col. Carabidae). *Ibid.*, 4: 372–388.
- Liebke, M. 1935. Neue Carabiden aus Süd-und Mittelamerika, hauptsächlich des Pariser Museums. Revue Francaise d'Entomologie, 2: 143–177.
- Liebke, M. 1936. Die Gattung *Lachnophorus* Dejean (Col. Carabidae). Revista de Entomología, 6: 461–468.
- Liebke, M. 1938. Denkschrift über die Carabiden-Tribus Colliurini. Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand, vol. 4, pp. 37–131.
- Liebke, M. 1939a. Neue Laufkäfer. Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand, vol. 5, pp. 91–130.
- Liebke, M. 1939b. Miscellanea carabidologica americana. Pars IV. Revista de Entomología, 10: 472–479.
- Liebherr, J. D. 1983. Larval description of *Calybe (Ega) sallei* Chevrolat with a preliminary assessment of lachnophorine affinities. Coleopterists Bulletin, 37: 254–260.
- Lindroth, C. H. 1954. Random notes on North American Carabidae (Coleopt.), Bulletin of the Museum of Comparative Zoology, 111: 117–161.
- Lindroth, C. H. 1961. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 2. Opuscula Entomologica, Supplementum 20, pp. 1–200.
- Lindroth, C. H. 1966. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 4. *Ibid.*, Supplementum 29, pp. 409–648.
- Lindroth, C. H. 1969a. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 6. *Ibid.*, Supplementum 34, pp. 945–1192.
- Lindroth, C. H. 1969b. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 1. *Ibid.*, Supplementum 35, pp. i–xlviii.
- Linné, C. von. 1758. Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, ed. 10, vol. 1, 823 pp. Holmiae.
- Linné, C. von. 1763. Centuria Insectorum rariorum. Resp. Boas Johansson. 4, pp. 384–415. Upsaliae.
- Linné, C. von. 1766. Systema naturae, vol. 1, pars 2, editio duodecima reformata, pp. 533–1327. Holmiae.
- Lutschnik, V.N. 1915. Sous-genre *Poecilus* (Bonelli) du genre *Platysma* (Bonelli) Tschitschérine et ses sections (Coleoptera, Carabidae). Revue Russe d'Entomologie, 14: 412–417.
- Lutschnik, V.N. 1922. On the Platysmatina. Acta Inst. Agronom., 14: 67–79.
- Lutschnik, V.N. 1929. Analecta Carabidologica. Acta Societatis Entomologicae Cechosloveniae, 26: 5–7.
- MacLeay, W. S. 1825. Annulosa javanica or an attempt to illustrate the natural affinities and analogies of the insects collected in Java by T. Horsfield, 50 pp., 1 pl. London.

- MacLeay, W. S. 1866. On the Scaritidae of New Holland. Transactions of the Entomological Society of New South Wales, 1: 55–91.
- Madge, R. B. 1967. A revision of the genus *Lebia* Latreille in American North Mexico (Coleoptera, Carabidae). Quaestiones Entomologicae, 3: 139–242.
- Mandl, K. 1971. Wiederherstellung des Familienstatus der Cicindelidae (Coleoptera). Beiträge zur Entomologie, 21: 507–508.
- Mannerheim, C. G. von. 1837. Mémoire sur quelques genres et espèces de carabidiques. Bulletin de la Société Impériale des naturalistes Moscou, 10(2): 3–49.
- Mateu, J. 1954. El género *Callidula* Chaudoir, Revista de la Sociedad Entomologica Argentina, 17: 3–8.
- Mateu, J. 1974. Sur les *Microlestes* Schmidt-Goebel du Mexique (Col. Carabidae Lebiinae). Entomologischen Arbeiten aus dem Museum G. Frey Tutzing beim München, 25: 261–278.
- Mateu, J. 1981. Revision de los *Zuphium* del continente Americano (Coleoptera: Carabidae) la. Nota. Folia Entomologica Mexicana, 47: 111–128.
- Ménétriés, E. 1844. Sur un envoi d'insectes de la côte N. O. d'Amérique. Bulletin de la Académie Impériale de Science de St.-Petersbourg, Classe Physico-Mathématique, 2: 49–64.
- Moore, B. P. 1964. Australian larval Carabidae of the subfamilies Broscinae, Psydriinae and Pseudomorphinae (Coleoptera). Pacific Insects, 6: 242–246.
- Moore, B. P. 1965. Australian larval Carabidae of the subfamilies Harpalinae, Licininae, Odacanthinae and Pentagonicinae (Coleoptera). Proceedings of the Linnean Society of New South Wales, 90: 157–163.
- Moore, B. P. 1979. Chemical defense in Carabids and its bearing on phylogeny. In, Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern eds, Carabid Beetles: Their evolution, natural history, and classification. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk, Publishers, The Hague. pp. 193–203.
- Morawitz, A. 1862. Vorläufige Diagnosen neuer Carabiden aus Hakodade. Mélanges Biologiques Tirés du Bulletin de l'Académie Impériale des Sciences de St.-Petersbourg, 4: 238–240.
- Motschulsky, T. V. von. 1839. Coléoptères du Caucase et des provinces Transcaucasiennes décrits par T. Victor. Bulletin de la Société Impériale des Naturalistes Moscou, 12: 68–93.
- Motschulsky, T. V. von. 1845. Insectes de la Sibirie. Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg, 13: 1–274.
- Motschulsky, T. V. von. 1846. Die Coleopterologischen Verhältnisse und die Käfer Russlands. 9 pp. Moscou.
- Motschulsky, T. V. von. 1847. Antwort an Dr. Gebler auf seiner bemerkungen in der Nr. II. u. IV des Bulletin 1847. Article I. Bulletin de la Société Impériale des naturalistes Moscou. 20: 218–228.
- Motschulsky, T. V. von. 1850. Die Käfer Russlands, 91 pp. tables I–XI. Moscou.
- Motschulsky, T. V. von. 1851. Enumeration des nouvelles espèces de Coléoptères rapportes. Bulletin de la Société Impériale des Naturalistes Moscou, 24: 479–511.
- Motschulsky, T. V. von. 1857. Études entomologiques. Helsingfors. vol. 6, pp. 1–112.
- Motschulsky, T. V. von. 1859. Coléoptères nouveaux de la Californie. Bulletin de la Société Impériale des Naturalistes Moscou, 32: 122–185.
- Motschulsky, T. V. von. 1861. Essai d'un catalogue des insectes de l'île Ceylan. Lief I. *Ibid.*, 34: 95–155.

- Motschulsky, T. V. von. 1862. Entomologie speciale. Remarques sur la collection d'insectes de V. de Motschulsky. Coléoptères. Études Entomologiques, 11: 15–55.
- Motschulsky, T. V. von. 1864. Énumération des nouvelles espèces de coléoptères rapportés de ses voyages. Bulletin de la Société Impériale des Naturalistes Moscou, 37(2): 171–240, 297–355. (4<sup>e</sup> article).
- Motschulsky, T. V. von. 1865. Énumération des nouvelles espèces de coléoptères rapportés de ses voyages. *Ibid.*, 38(4): 227–313. (4<sup>e</sup> article. Suite.).
- Müller, G. 1926. I Coleotteri della Venezia Giulia. Studi Entomologici, 1(2): 94–98.
- Mutchler, A. H. 1924. A new species of Cicindelidae from Cuba. American Museum Novitates, No. 106, pp. 1–3.
- Mutchler, A. H. 1934a. New species of Carabidae from Puerto Rico. *Ibid.*, No. 686, pp. 1–5.
- Mutchler, A. H. 1934b. Supplement. [New species of *Masoreus* from Puerto Rico and Cuba]. Psyche, 41: 130–131.
- Nègre, J. 1963. Revision du genre *Polpochila* Solier (Coleoptera: Carabidae) Revue Française d'Entomologie, 30: 205–241.
- Netolitzky, F. 1910. Bemerkungen zur Systematik in der Gattung *Bembidion* Latr. Wiener Entomologische Zeitung, 29: 209–228.
- Netolitzky, F. 1911. *Bembidion* Studien. *Ibid.*, 30: 170–194.
- Netolitzky, F. 1914a. Die Bembidiini in Winklers Catalogus. Zweite Mitteilung. Entomologische Blätter, 10: 164–176.
- Netolitzky, F. 1914b. Die Bembidiini in Winklers Catalogus. Zweite Mitteilung. *Ibid.*, 10: 50–55.
- Netolitzky, F. 1918. Neuv Bembidiini Europas (Carabidae). Koleopterologische Rundschau, 7: 19–25.
- Netolitzky, F. 1920. Zwei neue *Bembidion* -Untergattungen und eine neue Art. *Ibid.*, 8: 1–96.
- Netolitzky, F. 1931. Kritisches zum Katalog der Harpalinae von Csiki. Deutsche Entomologische Zeitschrift, 1931, pp. 153–167.
- Netolitzky, F. 1942. Bestimmungstabelle der *Bembidion* -Arten des palaarktischen Gebietes. Koleopterologische Rundschau, 28: 29–124.
- Nietner, J. 1858. Descriptions of new Ceylon Coleoptera. Annals and Magazine of Natural History, (ser. 3), 2: 418–431.
- Noonan, G. R. 1973. The Anisodactylines (Insecta: Coleoptera: Carabidae: Harpalini): classification, evolution, and zoogeography. Quaestiones Entomologicae, 9: 266–480.
- Noonan, G. R. 1976. Synopsis of the supra-specific taxa of the tribe Harpalini (Coleoptera: Carabidae). *Ibid.*, 12: 3–87.
- Notman, H. 1919. Records and new species of Carabidae. Journal of the New York Entomological Society, 27: 225–237.
- Notman, H. 1925. A review of the beetle family Pseudomorphidae, and a suggestion for a rearrangement of the Adephaga, with descriptions of a new genus and a new species. Proceedings of the United States National Museum, 67: 1–34.
- Notman, H. 1929. A new species of *Bembidion* from Lake Superior (Coleoptera, Carabidae). Journal of the New York Entomological Society, 37: 157–158.
- Ogueta, E. 1966. Las especies Americanas de *Panagaeus* Latreille, 1804 (Coleoptera, Carabidae). Physis, 26: 1–13.
- Ogueta, E. 1967. Las especies argentinas de la subfamilia Pseudomorphinae. G. Horn. Acta Zoológica Lilloana, 23: 217–232.



- Olivier, A. G. 1790. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coléoptères, vol. 2. Paris.
- Olivier, A. G. 1795. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coléoptères, vol. 3; vol. 4. Paris.
- Palisot de Beauvois, A. M. F. J. 1805. Insectes recueillis en Afrique et en Amérique, 1805–1821, 276 pp., 90 pls, Paris.
- Paykull, G. von. 1798. Fauna Suecica: Insecta, vol. 1, 358 pp. Upsaliae.
- Perty, J. A. M. 1830. Insecta Brasiliensia. Coleoptera Pentamera. Delectus animalium articulorum, quae in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I Bavariae regis augustissimi peracto, (fasc. 1), pp. 1–60. Monachii.
- Portevin, G. 1929. Histoire naturelle des Coléoptères de France. Tome 1. Adephaga – Polyphaga: Spaphylinoidea. Encyclopedie Entomologique Ser. A, x + 649 pp. Paris.
- Putzeys, J. A. A. H. 1845. Prémices entomologiques. Mémoires de la Société Royale des Sciences de Liège, 2(2), 1845/1846, pp. 353–417.
- Putzeys, J. A. A. H. 1846. Monographie des *Clivina* et genres voisins, précédée d'un tableau synoptique des genres de la tribu des scarities. *Ibid.*, pp. 521–663.
- Putzeys, J. A. A. H. 1863. Postscriptum ad clivinidarum monographiam atque de quibusdam aliis. *Ibid.*, 18:1–78.
- Putzeys, J. A. A. H. 1866. Révision générale des clivinides. Annales de la Société Entomologique de Belgique, 10: 1–242.
- Putzeys, J. A. A. H. 1874. Notice sur les cicindèles et carabiques recueillis dans l'Ile Antigua par M. Purves. *Ibid.*, 17: 117–119.
- Putzeys, J. A. A. H. 1878a. Description des *Selenophorus* de l'Amérique. Stettiner Entomologische Zeitung, 39: 3–73.
- Putzeys, J. A. A. H. 1878b. G. *Gynandropus* (Dej. spec. V.817). *Ibid.*, 39: 289–295.
- Randall, J. W. 1938. Descriptions of new species of coleopterous insects inhabiting the State of Massachusetts. Boston Journal of Natural History, 2: 34–52.
- Reichardt. H. 1967. A monographic revision of the American Galeritini (Coleoptera, Carabidae) Arquivos de Zoologia do Estado do São Paulo, 15: 1–176.
- Reichardt. H. 1968. Revisionary notes on the American Pentagoniciini (Coleoptera, Carabidae). Papéis Avulsos do Departamento de Zoologia, 21: 143–160.
- Reichardt. H. 1971a. Notes on the bombarding behaviour of three carabid beetles (Coleoptera, Carabidae). Revista Brasileira de Entomologia, 15: 31–34.
- Reichardt. H. 1971b. Carabidae (Coleoptera) neotropicais: espécies venezuelanas e formas relacionadas. Papéis Avulsos do Departamento de Zoologia, 25: 73–91.
- Reichardt. H. 1972a. A review of *Eurycoleus* Chaudoir (Coleoptera: Carabidae) *Ibid.*, 25: 237–249.
- Reichardt. H. 1972b. *Metaxidius* Chaudoir and the Neotropical Zuphiini (Coleoptera, Carabidae). *Ibid.*, 25: 265–268.
- Reichardt. H. 1974a. The South American Pogonini (Coleoptera, Carabidae). *Ibid.*, 27: 279–286.
- Reichardt. H. 1974b. Monograph of the Neotropical Helluonini, with notes and discussions of Old World forms (Coleoptera: Carabidae). Studia Entomologia, 17: 211–302.

- Reichardt, H. 1975. The genera of Salcediina (Coleoptera, Carabidae, Scaritini). *Revista Brasileira de Entomologia*, 19: 99–110.
- Reichardt, H. 1977. A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). *Quaestiones Entomologicae*, 13: 346–493.
- Reiche, L. 1842. Coléoptères de Colombie. *Revue Zoologique*, 1842, pp. 238–242, 272–276, 307–314, 374–378.
- Reiche, L. 1843. Coleoptera colombiana. *Ibid.*, 1843, pp. 37–41, 75–79, 141–145, 177–180.
- Reitter, E. 1896. Bestimmungs-Tabelle der europäischen Coleopteren: Enthaltend: Carabidae. I. Abtheilung: Carabini, gleichzeitig mit einer systematischen Darstellung sämtlicher Subgenus der Gattung *Carabus* L. *Verhandlungen der Naturforschenden Vereines in Brunn*, 34: 36–198.
- Reitter, E. 1900. Carabidae, Harpalini. In, *Best.-Tab. europ. Coleopt.*, *Ibid.*, 38: 33–144.
- Reitter, E. 1908. *Fauna Germanica. Die Käfer des deutschen Reiches. Nach 1 der analytischen Methode bearbeitet*, vol. 1, 248 pp., Stuttgart.
- Rivalier, E. 1950. Demembrement du genre *Cicindela* Linné. (Travail préliminaire limité à la faune paléarctique). *Revue Française d'Entomologie*, 17: 217–244.
- Rivalier, E. 1954. Demembrement du genre *Cicindela* Linné II. Faune americaine. *Ibid.*, 21: 249–268.
- Rivalier, E. 1955. Les *Brasiella* du groupe de *argentata* F. (Coleoptera, Cicindelidae). *Ibid.*, 22: 77–100.
- Rivalier, E. 1961. Demembrement du genre *Cicindela* Linné (Suite). IV. Faune Indomalaise. *Ibid.*, 28: 121–149.
- Rivalier, E. 1963. Demembrement du genre *Cicindela* Linné. V. Faune Australienne. (Et liste récapitulative des genres et sous-genres proposés pour la faune mondiale). *Ibid.*, 30: 30–48.
- Roeschke, H. 1900. Carabologische Notizen VI. *Entomologische Nachrichten*, 26: 68–72.
- Samouelle, G. 1819. *The entomologist's useful compendium*, 496 pp. London.
- Say, T. 1817. Descriptions of several new species of North American insects. *Journal of the Academy of Natural Sciences of Philadelphia*, 1: 19–23.
- Say, T. 1824. Coleoptera, In, *Narrative of an expedition to the source of St. Peter's River, &c., under the command of Stephen H. Long, Major U.S.T.E.*, vol. 2, pp. 268–378. Philadelphia.
- Say, T. 1825. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. *Transactions of the American Philosophical Society (ser. 2)*, 2: 1–109.
- Say, T. 1834. Descriptions of new North American insects and observations on some already described. *Ibid.*, 4: 409–470.
- Schaufuss, L. W. 1879. Neue Coleopteren-Arten und -Varietaten. *Nunquam otiosus*, III, 1879, pp. 552–557.
- Schaufuss, L. W. 1882. Coléoptères aveugles de la famille des Colydidae. *Annales de la Société Entomologique de France (ser. 6)*, 2: 46–48.
- Schaum, H. R. 1860a. *Naturgeschichte der Insecten Deutschlands*, Abth. 1, Coleoptera, vol. 1, pt. 1, pp. 1–791.
- Schaum, H. R. 1860b. Beiträge zur Kenntniss einiger Laufkafer-Gattungen. *Berliner Entomologische Zeitschrift*, 4: 180–203.
- Schaupp, F. G. 1883. Synoptic tables of Coleoptera. Cicindelidae. *Bulletin of the Brooklyn Entomological Society*, 6: 73–108.
- Schilder, F. A. 1953. Studien zur evolution von *Cicindela*. *Wissenschaftliche Zeitschrift der*

- Martin-Luther Universität Halle-Wittenberg. Mathematisch-Naturwissenschaftliche Reiche 3(2): 539-576.
- Schmidt-Goebel, H. M. 1846. Faunula coleopterorum Birmaniae, adjectis nonnullis Bengaliae indigenis, Lief. 1, pp. 1-94, pls. 1-3. Prague.
- Seidlitz, G. von. 1887. Fauna Baltica. Die Käfer (Coleoptera) der deutschen Ostseeprovinzen Russlands, 192 pp. Königsberg.
- Semenov-Tian-Shanskij, A. 1922. Carabinorum tribus Omophronina (Coleoptera) classificata. Conspectus praecursorius. Revue Russe d'Entomologie, 18: 36-45.
- Sloane, T. G. 1898. On Carabidae from West Australian, sent by Mr. A. M. Lea (with descriptions of new genera and species, synoptic tables, &c.). Proceedings of the Linnean Society of New South Wales, 23: 494pp.
- Solier, A. J. J. 1833. Observations sur les deux genres *Brachinus* et *Aptinus*, du sp cies de M. le Comte Dejean; et description d'une nouvelle esp ce de *Gyrinus*. Annales Soci t  Entomologique de France, 2: 459-463.
- Solier, A. J. J. 1848. Observations sur les genres *Procrustes*, *Procerus*, *Carabus* et *Calosoma*. Studi Entomologici Publicati per Cura di Flaminio Baudi e di Eugenio Trugui, 1: 48-62.
- Solier, A. J. J. 1849. Orden III. Coleopteros. In, Gay Historia fisica y politica de Chile, Paris. vol. 4, pp. 105-380.
- Steinheil, E. 1875. Beschreibung neuer Arten aus Columbia. Coleopterologische Hefte, 13: 95-103.
- Stephens, J. F. 1827. Illustrations of British entomology; or a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable, London, vol. 1, pp. 1-76, pls. 1-5.
- Stephens, J. F. 1828a. *Ibid.*, pp. 77-186, pls 6-9.
- Stephens, J. F. 1828b. *Ibid.*, vol. 2, pp. 1-112, pls. 10-14.
- Strand, E. 1929. Zoological and palaeontological nomenclatorial notes. Acta Universitatis Latviensis, 20: 3-29.
- Strand, E. 1936. Miscellanea nomenclatura zoologica et palaeontologica. Folia Zoologica et Hydrobiologica, 9: 167-170.
- Straneo, S. L. 1979. Notes about classification of the South American Pterostichini with a key for determination of subtribes, genera and subgenera (Coleoptera, Carabidae). Quaestiones Entomologicae, 15: 345-356.
- Sturm, J. 1826. Catalog meiner Insecten-S mmlung, Erster Theil, K fer, 207 pp., 4 pls. N rnberg.
- Sturm, J. 1843. Catalog der K fer-S mmlung von Jacob Sturm, 386 pp., 6 pls. N rnberg.
- Sulzer, J. H. 1776. Abgek rzte Geschichte der Insecten nach dem Linaeischen System, pt. 1, 274 pp.; pt. 2, 32 pls. Winterthur.
- Taglianti, A. V. 1973. The Anillini of Mexico and Guatemala (Coleoptera Carabidae). Quaderno, Accademia Nazionale dei Lincei, 171: 307-324.
- Thompson, R. G. 1977. A redescription of the larva of *Morion cordatus* Chaudoir (Coleoptera: Carabidae: Morionini). Coleopterists Bulletin, 30: 81-83.
- Thompson, R. G. 1979. Larvae of North American Carabidae with a key to the tribes. In, Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern eds, Carabid Beetles: Their evolution, natural history, and classification. Proceedings of the First International Symposium of Carabidology. Dr. W. Junk, Publishers, The Hague. pp. 209-291.

- Thomson, J. 1857a. Monographie des cicindélides ou exposé méthodique et critique des tribus, genres et espèces de cette famille, vol. 1, 66 pp., illus. Paris.
- Thomson, J. 1857b. Description de quatorze espèces nouvelles. Archives Entomologiques, 1: 129–136.
- Tschitschérine, T. 1896a. Note sur les *Derus* Motsch. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg, 1896, pp. 105–112.
- Tschitschérine, T. 1896b. Note sur deux nouvelles formes arctiques du genre *Feronia* Latr. Dej. *Ibid.*, 1896, pp. 373–377.
- Tschitschérine, T. 1897. Carabiques nouveaux ou peu connus. L'Abeille, 29:45–80.
- Tschitschérine, T. 1900. Notes sur les Platysmatini du Museum d'Histoire Naturelle de Paris. Horae Societatis Entomologicae Rossicae, 34: 371–397.
- Tschitschérine, T. 1901. Genera des Harpalini des régions paléarctique et Paléantartique. *Ibid.*, 35: 217–251.
- Tschitschérine, T. 1903. Nouvelles espèces de la tribu de Platysmatini. *Ibid.*, 36: 38–64.
- Van Dyke, E. C. 1918. A new genus and species of cave-dwelling Carabidae (Coleoptera) from the United States. Journal of the New York Entomological Society, 26: 179–182.
- Van Dyke, E. C. 1926. New species of Carabidae in the subfamily Harpalinae, chiefly from western North America. Pan-Pacific Entomologist, 2: 113–126.
- Vulcano, M. A. and F. S. Pereira. 1975. Os Rhysodidae Sul-americanos (Coleoptera). Studia Entomologia, 18: 153–188.
- Wasmann, E. 1929. Die Paussiden des baltischen Bernsteins und die Stammesgeschichte der Paussiden. Bernstein-Forschung, Heft 1, 110 pp.
- Waterhouse, C. O. 1878. Notice of a small collection of Coleoptera from Jamaica, with descriptions of new species from the West Indies. Transactions of the Entomological Society of London, 1878, pp. 303–311.
- Weber, F. 1801. Observationes entomologicae, continentes novorum quae condidit generum characteres, et nuper detectarum specierum descriptiones, 116 pp. Kiliae.
- Wesmael, C. 1845. Tentamen Dispositionis Methodicae Ichneumonum Belgii. Nouveaux Memoires de la Academie Royale des Sciences et Belle-Lettres de Bruxelles, 18: 1–235.
- Westwood, J. O. 1831. Mémoire pour servir a l'histoire naturelle de la famille des Cicindélites. Annales des Sciences Naturelles, 22: 209–317.
- Westwood, J. O. 1838. An introduction to the modern classification of insects; founded on the natural habits and corresponding organization of the different families, 2 volumes, 462 + 587 pp. London.
- Whitehead, D. R. 1966. A review of *Halocoryza* Alluaud, with notes on its relationship to *Schizogenius* Putzeys (Coleoptera, Carabidae). Psyche, 73: 217–228.
- Whitehead, D. R. 1969. Notes on *Dyschirius* Bonelli and *Akephorus* LeConte, with a peculiar new *Dyschirius* from Texas (Coleoptera: Carabidae: Scaritini). Journal of the New York Entomological Society, 77: 179–192.
- Whitehead, D. R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini), Quaestiones Entomologicae, 8: 131–348.
- Whitehead, D. R. 1973. Annotated key to *Platynus*, including *Mexisphodrus* and most "Colpodes" so far described from North America including Mexico (Coleoptera: Carabidae: Agonini). *Ibid.*, 9: 173–217.
- Whitehead, D. R. 1974. An annotated key to described species of the Neotropical genus *Glyptolenus* (Carabidae: Pterostichini: Agonini). Coleopterists Bulletin, 28: 123–132.

- Whitehead, D. R. and G. E. Ball. 1975. Classification of the middle American genus *Cyrtolaus* Bates (Coleoptera: Carabidae: Pterostichini). *Quaestiones Entomologicae*, 11: 591–619.
- Whitehead, D. R. and H. Reichardt. 1977. Classification of *Listropus* Putzeys, a subgenus of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). *Coleopterists Bulletin*, 31: 239–250.
- Wiegmann, A. F. A. 1835. Amphibien. *Beitrage zur Zoologie*, 17: 184–268.
- Wolcott, G. N. 1936. "Insectae Borinquenses." A revised annotated check-list of the insects of Puerto Rico. *The Journal of Agriculture of the University of Puerto Rico*, 20: 1–627.

## APPENDIX A: CHECKLIST OF THE SPECIES OF THE WEST INDIES

## I. CARABIDAE Latreille, 1810

Agridae Kirby 1837; Anchomenidae Laporte, 1834c; Anthiidae Hope, 1838; Apotomidae Jacquelin du Val, 1857; Bembidiidae Westwood, 1838; Brachinidae Bonelli, 1810; Broschidae Hope 1838; Callistidae Jeannel, 1941; Calpohaenidae Jeannel, 1942a; Chlaeniidae Westwood, 1838; Cnemacanthidae Lacordaire, 1854; Ctenodactylidae Laporte, 1834c; Cyclosomidae Hope, 1838; Cymbionotidae Jeannel, 1941; Dryptidae Laporte, 1834c; Elaphridae Stephens, 1827; Feronidae Laporte, 1834c; Gehrungiidae Darlington, 1933; Glyptidae Horn, 1881; Harpalidae MacLeay, 1825; Hiletidae Lacordaire, 1854; Lebiidae Bonelli, 1810; Licindae Bonelli, 1810; Loroceridae Bonelli, 1810; Masoreidae Chaudoir, 1876b; Melanodidae Jeannel, 1942b; Metriidae LeConte, 1861; Migadopidae Chaudoir, 1861; Nebriidae Laporte, 1834c; Odacanthidae Laporte, 1834c; Omophronidae Latreille, 1810; Orthogoniidae Chaudoir, 1871c; Ozaenidae Hope, 1838; Panagaeidae Bonelli, 1810; Patrobidae Kirby, 1837; Paussidae Latreille, 1806; Peleciidae Horn, 1881; Pentagoniidae Bates, 1873; Pericalidae Hope, 1838; Perigonidae Horn, 1881; Pseudomorphidae Horn, 1881; Psydridae LeConte, 1861; Pterostichidae Erichson, 1837; Scaritidae Bonelli, 1810; Siagonidae Bonelli, 1810; Thyreopteridae Chaudoir, 1869; Trechidae Bonelli, 1810; Zuphiidae Jeannel, 1941.

## SUBFAMILY CARABINAE

## SUPERTRIBE Carabitae

## TRIBE Carabini

**Calosoma** Weber 01–20

*Castrida* Motschulsky 65–300  
*Callistriga* Motschulsky 65–307  
*Calamata* Motschulsky 65–307  
*Acampalita* Lapouge 29a–9  
*Catastriga* Lapouge 29a–9  
*Callipara* Motschulsky 65–309  
*Syncalosoma* Breuning 27–144  
*Calodrepa* Motschulsky 65–310  
*Acamegonia* Lapouge 24–38  
*Camedula* Motschulsky 65–303  
*Carabosoma* Gehin 85–32  
*Camegonia* Lapouge 24–38  
*Chrysostigma* Kirby 37–19  
*Tapinosthenes* Kolbe 95–56  
*Lyperostenia* Lapouge 29a–3  
*Callitropa* Motschulsky 65–300  
*Paratropa* Lapouge 29a–3  
*Paracalosoma* Breuning 27–141  
*Blaptosoma* Gehin 85–33  
*Microcalosoma* Breuning 27–146  
*Neocalosoma* Breuning 27–146

*Aulacopterus* Gehin 85–34  
*Carabomimus* Kolbe 95–57  
*Calopachys* Haury 80–164  
*Eutelodontum* Gehin 81–82  
*Callisthenes* Fischer von Waldheim 21–10  
*Microcallisthenes* Apfelbeck 18–161  
*Isotenia* Lapouge 29a–2  
*Callistenia* Lapouge 29a–2

sayi Dejean 26–198. West Indies, C. Am., No. Am., Puerto Rico

*armatus* Laporte 35–156  
*abdominale* Gehin 85–58  
*virginicum* Casey 97–344  
*cuprascens* Roeschke 00–71

splendidum Dejean 31–558. (2) GA, FL; Cuba, Dominican Republic

**Carabus** Linné 58–413

*Megodontus* Solier 48–58  
*Diocarabus* Reitter 96–185  
*Hemicarabus* Gehin 85–19  
*Oreocarabus* Gehin 85–26  
*Cryocarabus* Lapouge 31–575  
*Eucarabus* Gehin 76–19  
*Neocarabus* Lapouge 31–569  
*Archicarabus* Seidlitz 87–6  
*Tanaocarabus* Reitter 96–135  
*Homoeocarabus* Reitter 96–144  
*Paracarabus* Lapouge 32–630  
*Neocarabus* Hatch 49a–144  
*Autocarabus* Seidlitz 87–7  
*Lichnocarabus* Reitter 96–161

basilicus Chevrolat 36–169. Puerto Rico

**SUPERTRIBE** Cicindelitae

**TRIBE** Megacephalini

**Megacephala** Latreille 02–79

*Metriocheila* Thomson 57a–50 (Subg)  
*Phaeoxantha* Chaudoir 50a–7 (Subg)  
*Tetracha* Hope 38–6

acutipennis Dejean 25–13. Cuba, Hispaniola, Puerto Rico

*adonia* Laporte 34a–83  
*cyaneo-nigra* Chaudoir (Leng & Mutchler 16–685)  
*laportei* Chevrolat 34a–83  
*virginica* Olivier 90–30

carolina Linné 66–657. BJ, MX Guatemala, Nicaragua, Cuba,  
 Grand Cayman, USA

*boisduvali* Gistel 37–7

*carolinensis* Latreille 06–175  
*maculicornis* Laporte 34b–29  
*mexicana* Gray 32–263  
*occidentalis* Klug 29–11  
*splendida* Dokhtouroff 82–46  
*virgula* Thomson 57a–31

rutilans Thomson 57a–35. Brazil

s. confusa Chaudoir 65–63. Colombia, Venezuela, Curaçao, Anegada,  
 St. Martin, Antigua

*antiguana* Leng & Mutchler 16–684

s. infusca Mannerheim 37–6. Cuba, Hispaniola, Puerto Rico, St. Thomas,  
 St. John, St. Croix, St. Martin, St. Barthélemy, USA

*obscurata* Chaudoir 44–454

# TRIBE Cicindelini

## Cicindela Linné 58–407

*Pentacomia* Bates 72b–265. (Subg)

acuniae Mutchler 24–1. Cuba

argentata Fabricius 01–242. MX, Guatemala, Costa Rica, Panamá, Colombia,  
 Venezuela, Br. Guiana, Fr. Guiana, Brazil, Bolivia, Argentina, Haiti,  
 Guadeloupe, Argentina, Haiti, Guadeloupe

*egaensis* Thomson 57b–130

*guerin* Gory 33–178

*lucorum* Gistel 37–71

*misella* Chaudoir 54–121

*pallipes* Fleutiaux & Sallé 89–359

*taitenis* Boheman 58–1

boops Dejean 31–258. Cuba, Hispaniola, Puerto Roco

cardini Leng & Mutchler 16–689. Cuba

cubana Leng & Mutchler 16–689. Cuba

dorsalis Say 17–20. MX, Cuba

p. castissima Bates 84–260

p. venusta Laferté-Senectère 41–37

*saucyi* Schaupp 83–99

longilabris Say 24–268. ID, UT, ID, IL, NY, NF, AK, CA, NE, WY, OR;  
 Canada, Bermuda?

marginata Fabricius 75–226. Bahamas Is, Cuba, USA

*variegata* Dejean 25–84

olivacea Chaudoir 54–118. Cuba, USA

rufiventris Dejean 25–102. Hispaniola, USA

*collusor* Casey 13–15

schaefferi Horn 03–213. MX, Haiti

suturalis Fabricius 98–62. S. Am., Hispaniola, Puerto Rico, St. Thomas,  
 St. John, St. Martin, St. Barthélemy, Barbuda, Antigua, Guadeloupe,  
 Martinique, Barbados, St. Vincent, Grenada



- p. *hebraea* Klug 34–20. S. Am., Dominican Republic, Puerto Rico, Antigua  
*chlorocephala* Mannerheim 37–17  
*hieroglyphica* Klug 34–30  
*trifasciata* Dejean 25–85  
*tropicalis* Motschulsky (Horn 26–173)
- p. *nocturna* Steinheil 75–96. S. Am., Guadeloupe  
*guadeloupensis* Fleutiaux & Sallé 89–358
- trifasciata* Fabricius 81–286. Bahamas, Cuba, I. de Pinos, Grand Cayman,  
 Jamaica, Hispaniola, Puerto Rico, St. Thomas, St. John, St. Martin,  
 Barbuda, Antigua, Guadeloupe, St. Barthélemy, Anguilla, St. Croix,  
 St. Domingo, Haiti, Virgin Is.  
*tortuosa* Dejean 25–87  
*hebraea* Putzeys 74–117
- s. *ascendens* LeConte 51–172. MX, Bahamas Is., USA  
*serpens* LeConte 51–173  
*sigmoidea* Chaudoir 54–113  
*tortuosa* LeConte 51–172  
*trifasciata* LeConte 48–181
- f. *sigmoidea* LeConte 51–172. MX?, St. John, USA  
*viridicollis* Dejean 31–265. Cuba  
*viridiflavescens* Horn 23–329. Dominican Republic  
 s. *originalis* Horn 36–23. Haiti

## SUBFAMILY SCARITINAE

## SUPERTRIBE Siagonitae

## TRIBE Enceladini

**Enceladus** Bonelli 13–460

*gigas* Bonelli 13–460. Brazil, Colombia, Surinam, French Guiana, Montserrat

## SUPERTRIBE Pseudomorphytae

## TRIBE Pseudomorphyini

**Pseudomorpha** Kirby 25–98

*Heteromorpha* Kirby 25–109

*Axinophorus* Dejean & Boisduval 29–60

*Drepanus* Dejean 31–434

*caribbeana* Darlington 35b–214. Haiti

## SUPERTRIBE Scarititae

## TRIBE Scaritini

**Scarites** Fabricius 01–123

*Scallophorites* Motschulsky 57–95

*Antilliscaris* Bänninger 49–136

*Taeniolobus* Chaudoir 55–30

cubanus Bänninger 37–321. Cuba  
 danforthi Darlington 39–80. Puerto Rico  
 darlingtoni Bänninger 35–159. Haiti  
 mutchleri Bänninger 39–149. Puerto Rico  
 megacephalus Hlavac 69–4. Puerto Rico  
 subterraneus Fabricius 75–249. ON, PA, DE; (2) SC, FL; (3) CA, MX; (5) SD;

Cuba

*fosser* Degeer 74–350

*spinipes* Sulzer 76–62

*interruptus* Herbst 84–133

*subterraneus* Bonelli 13–466

*beckwithi* Stephens 27–37

*denticollis* Chaudoir 43–729

s. patruelis LeConte 45–207. (2) GA, FL; Cuba

s. alternans Chaudoir 43–729. (2) ?FL, Cuba

montana Mutchler 34a–1. Puerto Rico

**Stratiotes** Putzeys 46–522

iracunda Putzeys 63–9. Dominica, Martinique

TRIBE Clivinini

**Dyschirius** Bonelli 13–483

*Akephorus* LeConte 51–194

*Dyschiridius* Jeannel, 41–264

erythrocerus LeConte 57–78. (1) NF, ON, IN, OH, DE, NY; (2) FL; (5) SD,  
 (3) MX; Cuba

coamensis Mutchler 34a–2. Puerto Rico

sublaevis Putzeys 46–562. (1) NY; (3) TX, MX; (5) MB; Cuba

*rubiventris* LeConte 57–79

*dentiger* LeConte 57–79

**Clivina** Latreille 02–96

*Eupalamus* Schmidt-Goebel 46–pl. 3

*Isoclivina* Kult 59–117

*Paraclivina* Kult 47–31

*Semiclivina* Kult 47–31

dentipes Dejean 25–415. (1) DE; (2) SC, GA, FL; (3) TX, AZ, CA; Cuba

bipustulata Fabricius 01–125. (1) ON, PA, DE; (2) SC, FL; (3) AZ, MX;  
 (5) SD; West Indies, Cuba

*quadrimaculata* Palisot de Beauvois 05–107

addita Darlington 34–67. Puerto Rico

biguttata Putzeys 66–155. Cuba

*bisignata* Leng & Mutchler 14–395

cubae Darlington 34–68. Cuba

insularis Jacquelin du Val 57–13. Cuba, Puerto Rico

limbipennis Jacquelin du Val 57–16. Cuba, Puerto Rico

*simplex* Chevrolat 63–192

- marginipennis Putzeys 46–619. (3) MX; “USA”; Guadeloupe  
**Halocoryza** Alluaud 19–100  
 arenaria Darlington 39–84. (2) FL; (3) MX; Dominican Republic  
**Schizogenius** Putzeys 46–649  
     *Genioschizus* Whitehead 72–144  
     *Listropus* Putzeys 63–3  
 arimao Darlington 34–71. Cuba  
**Oxydrepanus** Putzeys 66–103  
 rufus Putzeys 46–564. (2) FL; Cuba, Guadeloupe  
     *brevicarinatus* Putzeys 46–571  
 reicheoides Darlington 39–83. Dominican Republic  
**Neoreicheia** Kult 50–322  
     [See *Oxydrepanus*]  
**Ardistomis** Putzeys 46–636  
     *Semiardistomis* Kult 50–301  
     *Ardistomiellus* Kult 50–303  
 atripennis Putzeys 66–202. Guadeloupe  
 cyaneolimbatus Chevrolat 63–194. Cuba  
     *gundlachi* Leng & Mutchler 14–395  
 elongatulus Putzeys 66–208. Cuba  
 laevistriatus Fleutiaux & Sallé 89–363. Guadeloupe  
 mannerheimi Putzeys 46–645. Puerto Rico  
 nigroclarus Darlington 39–83. Dominican Republic  
 nitidipennis Darlington 34–70. Cuba  
 ramsdeni Darlington 37a–120. Cuba  
 rufoclarus Darlington 39–82. Dominican Republic  
 guadeloupensis Kult 50–307. Guadeloupe  
 alticola Darlington 35b–173. Haiti  
**Aspidoglossa** Putzeys 46–626  
 aerata Putzeys 46–635. West Indies  
 semicrenata Chaudoir 43–735. Guadeloupe  
     *guadeloupensis* Putzeys 46–632  
 vulnerata Putzeys 46–633. Puerto Rico Cuba, S. Am.  
     *comma* Putzeys 46–634

## SUBFAMILY PAUSSINAE

## SUPERTRIBE Paussitae

## TRIBE Ozaenini

- Pachyteles** Perty 30–3  
 delauneyi Fleutiaux & Sallé. 89–362 Guadeloupe  
 gyllenhali Dejean 25–436. Cuba, S. Am.  
     *pallida* Chevrolat 63–190

## SUPERTRIBE Brachinitae

## TRIBE Brachinini

**Brachinus** Weber 01–22*Brachynus auctorum**Neobrachinus* Erwin 70–47

brunneus Laporte 35–59. Cuba, Dominican Republic, Haiti, Puerto Rico,  
Virgin Is., Costa Rica, French Guiana

*gilvipes* Mannerheim 37–41

adustipennis Erwin 70–81. (1) MI, NY, MA, IL, IN; (2) TN, GA, FL, AL, AR,  
MS, LA; (3) OK, TX, NM, MX; (5) KS, MO; Panamá, Cuba

**Pheropsophus** Solier 33–463*Pheropsophidius* Hubenthal 11–547*Protopheropsophus* Hubenthal 11–548

aequinoctialis Linné 63–395. (3) MX; Nicaragua, Costa Rica, Panamá,  
Trinidad, Hispaniola, S. Am.

*complanatus* Fabricius 75–242*planus* Olivier 95–62*obliquus* Brullé 34a–251

## SUBFAMILY PSYDRINAE

## SUPERTRIBE Rhysoditae

## TRIBE Rhysodini

**Clinidium** Kirby 35–6*Mexiclinidium* Bell & Bell 78–63*Protainoa* Bell & Bell 78–63*Tainoa* Bell & Bell 78–64*Arctoclinidium* Bell 70–308

xenopodium Bell 70–316. Dominican Republic

darlingtoni Bell 70–317. Jamaica

curvicosta Chevrolat 73–215. Cuba

incis Bell 70–319. Puerto Rico

guldingi Kirby 35–8. St. Vincent, Cuba, Guadeloupe

planum Chevrolat 44–58. Guadeloupe

humidens Chevrolat 73–215. Cuba

boroquense Bell 70–321. Puerto Rico

haitiense Bell 70–322. Haiti

jamaicense Arrow 42–181. Jamaica

chiolinoi Bell 70–323. Jamaica

**Plesioglymmius** Bell & Bell 78–70*Ameroglymmius* Bell and Bell 79–435

compactus Bell & Bell 79–437. Cuba

## SUPERTRIBE Trechitae

## TRIBE Trechini

**Perileptus** Schaum 60a–663

columbus Darlington 34–86. Cuba

dentifer Darlington 35b–177. Haiti, Puerto Rico

jeanneli Darlington 34–87. Jamaica

minutus Darlington 35b–178. Jamaica, Haiti

## TRIBE Pogonini

**Diplochaetus** Chaudoir 71b–43

rutilus Chevrolat 63–197. Cuba, S. Am.

## TRIBE Bembidiini

**Mioptachys** Bates 82–144*Tachymenis* Motschulsky 62–27 (not Weigmann)

autumnalis Bates 82–137. (3) MX; Guatemala, Nicaragua, Panamá, Cuba,

Montserrat, Guadeloupe

insularis Darlington 39–86. Dominican Republic

noctis Darlington 35b–174. Haiti

**Tachyta** Kirby 37–56

hispaniolae Darlington 34–77. Haiti

**Elaphropus** Motschulsky 39–73*Tachylopha* Motschulsky 62–27*Tachyura* Motschulsky 62–27*Barytachys* Chaudoir 68b–213*Sphaerotachys* Müller, 26–95*Trepanotachys* Alluaud 33–17*Tachyphanes* Jeannel 46–362

tritax Darlington 35b–175. Haiti

yunax Darlington 39–87. Dominican Republic, Cosmop.

**Pericompsus** LeConte 51–191*Tachysops* Casey 18a–171*Tachysalia* Casey 18a–173*Leiotachys* Jeannel 62–616*Eidocompsus* Erwin 74b–21*Leptotachys* Jeannel 62–615immaculatus Bates 71b–246. (3) MX; Honduras, Costa Rica, Panamá, Cuba,  
S. Am.reichei Putzeys 45–415. (3) MX; Guatemala, Honduras, Costa Rica, Panamá,  
Jamaica, S. Am.

jamcubanus Erwin 74b–57. Jamaica, Cuba

elegantulus Laferté-Sénéctère 41–46. Puerto Rico

*blandulus* Schaum 60b–202

macrodentra Chevrolat? (Wolcott 36–187) Puerto Rico  
 morantensis Erwin 74b–61. Jamaica, Haiti, Dominican Republic  
 philipi Erwin 74b–62. Haiti

**Tachys** Stephens 28b–4

*Isotachys* Casey 18a–204  
 bradycellinus Hayward 00–224 (2) LA; Cuba, Haiti, Jamaica  
 translucens Darlington 34–123. Cuba  
 vittiger LeConte 51–193. (3) CA; Puerto Rico, Antigua, Galapagos  
*ensenadae* Mutchler 34a–3

**Paratachys** Casey 18a–174

*Eotachys* Jeannel 41–426  
 abruptus Darlington 34–80. Guadeloupe  
 albipes LeConte 63–20. (2) LA: Guadeloupe  
*putzeysi* Fleutiaux & Sallé 89–363  
 carib Darlington 35b–176. Haiti, Puerto Rico  
 cubax Darlington 34–78. Cuba  
 dominicanus Darlington 34–81. Dominica  
 filax Darlington 34–83. Cuba  
 paulax Darlington 34–80. Cuba  
 piceolus Laferté-Sénéctère 41–48. Puerto Rico  
 striax Darlington 34–82. Cuba

**Polyderis** Motschulsky 62–27

*Microtachys* Casey 18a–210  
*Neotachys* Kult 61–2  
*Polyderidius* Jeannel 62–611  
 ridiculus Schaufuss 79–552. St. Thomas, Virgin Islands, Guatemala, Cuba  
*capito* bates 84–287

**Lymnastis** Motschulsky 62–27

*Paralimnastis* Jeannel 32–176  
*Limnastis auctorum*  
 americana Darlington 34–83. Cuba

**Micratopus** Casey 14a–42

*Blemus* LeConte 48–473  
 insularis Darlington 34–86. Puerto Rico  
 parviceps Darlington 34–85. Cuba

**Stylulus** Schaufuss 82–46

*Petrocharis* Ehlers 84–36  
 nasutus Schaufuss 82–46. St. Thomas  
*eggersi* Ehlers 84–36

**Bembidion** Latreille 02–82

*Chrysobracteon* Netolitzky 14a–166  
*Parabracteon* Notman 29–157  
*Bracteon* Bedel 79–27  
*Odontium* LeConte 48–452  
*Ochthedromus* LeConte 48–453  
*Hydrium* LeConte 48–453

*Eudromus* Kirby 37–55  
*Eurytrachelus* Motschulsky 46–tab. 5  
*Pogonidium* Ganglbauer 92–149  
*Bracteomimus* Lindroth 54–144  
*Metallina* Motschulsky 46–tab. 5  
*Actedium* Motschulsky 64–182  
*Lionepha* Casey 18a–18  
*Trechonepha* Casey 18a–19  
*Plataphodes* Ganglbauer 92–152  
*Plataphus* Motschulsky 64–184  
*Micromelomalus* Casey 18a–37  
*Melomalus* Casey 18a–37  
*Blepharoplataphus* Netolitzky 20–96  
*Trichoplataphus* Netolitzky 14b–51  
*Trachelonepha* Casey 18a–37  
*Liocosmius* Casey 18a–43  
*Leuchydrium* Casey 18a–46  
*Pseudoperyphus* Hatch 50–100  
*Bembidionetolitzkyi* Strand 29–25  
*Daniela* Netolitzky 10–210  
*Peryphus* Stephens 28b–2  
*Hydriomicrus* Casey 18a–87  
*Eupetedromus* Netolitzky 11–190  
*Notaphus* Stephens 28b–51  
*Peryphodes* Casey 18a–85  
*Furcacampa* Netolitzky 31–158  
*Lopha* Stephens 28b–2  
*Cyclolopha* Casey 18a–144  
*Semicampa* Netolitzky 10–217  
*Diplocampa* Bedel 96–70  
*Parabopha* Casey 18a–153  
*Trepanedoris* Netolitzky 18–24  
*Amerizus* Chaudoir 68b–216  
*Philochthus* Stephens 28b–7  
*Cylindrobracteon* Netolitzky 42–50  
*Litoreobracteon* Netolitzky 42–51  
*Argyrobracteon* Netolitzky 42–53  
*Conicibracteon* Netolitzky 42–53  
*Stylobracteon* Netolitzky 42–53  
*Foveobracteon* Netolitzky 42–54  
*Desarmatocillenus* Netolitzky 42–39  
*Peryphophila* Netolitzky 42–64  
*Chinocillenus* Netolitzky 42–41  
*Philochthemphanes* Netolitzky 42–82  
*Hirmoplataphus* Netolitzky 42–107  
*Aureoplataphus* Netolitzky 42–108

*Synechoperyphus* Netolitzky 42–122

*Lymneops* Casey 18a–168

*cubanum* Darlington 37a–121. Cuba

*jamaicense* Darlington 34–76. Jamaica

*portoricense* Darlington 39–86. Puerto Rico

*rucillum* Darlington 39–86. ~~Puerto Rico~~ DR

*turquinum* Darlington 37a–122. Cuba

*sparsum* Bates 82–151. (3) MX; Nicaragua, Guatemala, Cuba, Puerto Rico, S. Am.

*spretum* Dejean 31–70. (3) MX; Haiti, Puerto Rico, Antigua

*fastidiosus* Laferté-Sénéctère 41–49

*apicale* Jacquelin du Val 56–23

*chevrolati* Gemminger & Harold 68–409

*viridicollis* Laferté-Sénéctère 41–48. (2) FL; (3) TX, MX; (4) AZ; (5) NW, AB, SA, MB, SD; Cuba, Puerto Rico

*hamiferum* Chaudoir 68b–244

*apicale* Jacquelin du Val 56–23

*chevrolati* Gemminger & Harold 68–409

*particeps* Casey 18a–124

*affine* Say 25–86. (1) ON, MI, DE; (2) SC, AL, Cuba; (3) TX; (5) SD

*decipiens* Dejean 31–159

*fallax* Dejean 31–189

*thespis* Casey 18a–128

*darlingtoni* Mutchler 34a–3. Puerto Rico, Cuba

## SUBFAMILY HARPALINAE

### SUPERTRIBE Pterostichitae

#### TRIBE Morionini

#### Morion Latreille 10–159

*Morio auctorum*

*costigerus* Darlington 34–90. Jamaica

#### TRIBE Pterostichini

#### Agonum Bonelli 10–syn. tab.

*Anchomenus auctorum*

*Paranchomenus* Casey 20a–30

*Anchomenus* Samouelle 19–106

*Pseudanchus* Casey 20a–45

*Taphranchus* Casey 20a–52

*Stictanchus* Casey 20a–54

*Idiochroma* Bedel 02–216

*Deratanchus* Casey 20a–70

*Circinalia* Casey 20a–72

*Circinalidia* Casey 20a–78



*Micragonum* Casey 20a–80

*Stereagonum* Casey 20a–80

*Tetraleucus* Casey 20a–88

*Platynomicrus* Casey 20a–90

*Leucagonum* Casey 20a–99

*Melanagonum* Casey 20a–111

*Paragonum* Casey 20a–123

*Punctagonum* Grey 37–311

*Europhilus* Chaudoir 59a–124

*Tanystola* Motschulsky 50–69

*Anchus* LeConte 54–38

*Oxypselaphus* auctorum

*coptoderoides* Darlington 37a–134. Cuba

*extensicolle* Say 25–54. (1) NS, PA, DE; (3) MX; (5) MB, SD

*proximum* Harris 28–132

*obscuratum* Chaudoir 43–763

*viride* LeConte 48–222

*gaudens* Casey 20a–55

*clientulum* Casey 20a–55

*vigilans* Casey 20a–56

*elongatulum* auctorum

*simplex* LeConte 54–46

*cyanescens* Motschulsky 59–159

*s. cubanum* Darlington 34–97. Cuba

*laetificum* Darlington 35b–200. Haiti

**Platynus** Bonelli 10–syn. tab.

*Anchomenus* auctorum

*Colpodes* auctorum

*Dyscolus* Dejean 31–347

*Metallosomus* auctorum

*Stenocnemus* Mannerheim 37–29

*Rhadine* LeConte 48–218

*Ophryodactylus* Chaudoir 50b–382

*Limodromus* Motschulsky 64–316

*Comstockia* Van Dyke 18–179

*Platynidius* Casey 20a–4

*Macragonum* Casey 20a–4

*Hemiplatynus* Casey 20a–15

*Stenoplatynus* Casey 20a–15

*Anacolpodes* Casey 20a–17

*acunia* Darlington 37a–133. Cuba

*agonella* Darlington 35b–187. Haiti

*alternans* Chaudoir 78b–348. Guadeloupe

*altifluminis* Darlington 35b–198. Haiti

*amone* Darlington 35b–190. Haiti

*aequinoctialis* Chaudoir 50b–383. (3) MX, West Indies, S. Am.

- baragua Darlington 35b-197. Cuba  
 biramosa Darlington 39-89. Dominican Republic  
 s. transcribao Darlington 39-91. Dominican Republic  
 s. uniramosa Darlington 39-90. Dominican Republic  
 bromeliarum Darlington 37b-122. Jamaica  
 bruesi Darlington 35b-196. Jamaica  
 bruneri Darlington 37a-132. Cuba  
 bucheri Darlington 37a-130. Cuba  
 calathina Darlington 39-92. Dominican Republic  
 carabiai Darlington 37a-129. Cuba  
 chalybaea Dejean 31-720. Guadeloupe, S. Am.  
 christophe Darlington 35b-191. Haiti  
 cinchonae Darlington 34-93. Jamaica  
 constricticeps Darlington 35b-194. Haiti  
 cubensis Darlington 37a-132. Cuba  
 cuprascens Motschulsky 64-305. Hispaniola  
 cychrina Darlington 35b-192. Haiti  
 dejeani Chaudoir 59b-359. Guadeloupe  
     *brunnea* Dejean 31-440  
 elliptica Chaudoir 78b-312. Guadeloupe, Martinique, S. Am.  
 elongata Chaudoir 78b-344. Guadeloupe  
 estriata Darlington 39-96. Puerto Rico  
 faber Darlington 35b-185. Jamaica  
 fractilinea Darlington 34-96. Haiti  
 fratrorum Darlington 37a-129. Cuba  
 jaegeri Dejean 31-728. Hispaniola  
 laeviceps Darlington 39-91. Dominican Republic  
 latelytra Darlington 35b-199. Jamaica  
 l'herminieri Chaudoir 42-838. Guadeloupe  
 macer Darlington 34-94. Jamaica  
 mannerheimi Chaudoir 59b-360. Hispaniola  
     *jaegeri* Mannerheim 37-30  
 marca Darlington 35b-180. Haiti  
 media Darlington 37a-130. Cuba  
 mediotra Darlington 37a-130. Cuba  
 memnonia Dejean 31-439. Guadeloupe  
 pavens Darlington 35b-188. Haiti  
 pinarensis Darlington 37a-128. Cuba  
 puncticeps Darlington 39-94. Dominican Republic  
 s. compacta Darlington 39-95. Dominican Republic  
 punctus Darlington 35b-195. Jamaica  
 ramoni Darlington 39-92. Dominican Republic  
 roysi Darlington 37b-124. Jamaica  
 scripta Darlington 39-93. Dominican Republic  
 scriptella Darlington 39-94. Dominican Republic  
 sellensis Darlington 37b-122. Haiti

subangusta Darlington 37a–131. Cuba  
 subcordens Darlington 35b–192. Haiti  
 subovalis Darlington 35b–186. Jamaica  
 tipoto Darlington 35b–193. Haiti  
 turquinensis Darlington 37a–131. Cuba  
 vagepunctata Darlington 34–95. Jamaica  
 visitor Darlington 35b–195. Haiti  
 wolla Darlington 35b–189. Haiti

**Glyptolenus** Bates 78–595

*Glyptoglenus* Bertkau 78–428  
 simplicicollis Darlington 34–97. Dominica  
 chalybaeus Dejean 31–720. Nicaragua, Costa Rica, Panamá, Guadeloupe,  
 Dominica, S. Am.  
*lebioides* Bates 78–599

**Dyschromus** Chaudoir 35–429

centralis Darlington 39–88. Dominican Republic  
 cupripennis Chaudoir 74–18. Hispaniola  
 opacus Chaudoir 35–430. Hispaniola  
 perezi Darlington 39–88. Dominican Republic  
 tiburonicus Darlington 35b–179. Haiti

**Pterostichus** Bonelli 10–syn. tab.

*Platysma* Bonelli 10–syn. tab.  
*Feronia* Latreille 17–101  
*Cylindrocharis* Casey 18b–326  
*Holciophorus* LeConte 52–249  
*Hypherpes* Chaudoir 38–8  
*Brachystilus* Chaudoir 38–10  
*Haplocoelus* Chaudoir 38–8  
*Gonoderus* Motschulsky 59–149  
*Monoferonia* Casey 18b–322  
*Leptoferonia* Casey 18b–321  
*Gastrellarius* Casey 18b–321  
*Orsonjohnsonus* Hatch 33–119  
*Steropus* Stephens 28a–116  
*Steroderus* Motschulsky 50–tab. 9  
*Derus* Motschulsky 50–50  
*Derulus* Tschitschérine 96a–112  
*Poecilus* Bonelli 10–syn. tab.  
*Leconteus* Lutschnik 15–414  
*Parapoecilus* Jeannel 42a–751  
*Bothriopterus* Chaudoir 38–9  
*Dysidius* Chaudoir 38–8  
*Parargutor* Casey 18b–324  
*Euferonia* Casey 18b–322  
*Omaseidius* Jeannel 42a–784  
*Refonia* Casey 18b–323

*Piesmus* LeConte 48–340  
*Ophryogaster* Chaudoir 78a–59  
*Pristoscelis* Chaudoir 78a–71  
*Lophoglossus* LeConte 52–248  
*Melanius* Bonelli 10–syn. tab.  
*Pseudomaseus* Chaudoir 38–10  
*Metamelanius* Tschitschérine 00–395  
*Lagarus* Chaudoir 38–10  
*Platyderus* Kirby 37–29  
*Pseudargutor* Casey 18b–324  
*Pseudolagarus* Lutschnik 22–70  
*Argutor* Stephens 28a–102  
*Micromaseus* Casey 18b–324  
*Omaseulus* Lutschnik 29–5  
*Americomaseus* Csiki 30–644  
*Cryobius* Chaudoir 38–11  
*Pseudocryobius* Motschulsky 50–9  
*Lyperopherus* Moschulsky 45–156  
*Euryperis* Motschulsky 50–9  
*Stereocerus* Kirby 37–34  
*Boreobia* Tschitschérine 96b–373  
*Hammatomerus* Chaudoir 68b–337  
*Pheryphes* Casey 20b–186  
*Feronina* Casey 18b–222  
*Anilloferonia* Van Dyke 26–115  
*Peristhethus* LeConte 73–305  
*Gastrosticta* Casey 18b–323  
*Paraferonia* Casey 18b–323  
*Allotriopus* Bates 82–81  
*Pseudoferonina* Ball 65–107  
*Melvilleus* Ball 65–110  
*Mayaferonia* Ball & Roughley 82–335

*cubensis* Darlington 37a–123. Cuba

*chalcites* Say 25–56. Cuba, USA

*cupreomicans* Sturm 43–23

*micans* Chaudoir 43–767

*sayi* Brullé 35a–277

**Caelostomus** MacLeay 25–23

*punctifrons* Chaudoir 50b–430. Jamaica, (W. Africa)

**Loxandrus** LeConte 52–250

*Megalostylus* Chaudoir 43–765

*infimus* Bates 82–87. (3) TX, MX; Haiti

*mutans* Darlington 35b–180

*rectangulus* LeConte 78–377. (2) FL; (3) TX, MX; Grand Cayman Island

*celeris* Dejean 28–246. (2) SC, GA, FL, AL, LA, MS; (3) TX, MS; Bahamas,

Cuba, Puerto Rico

*cruentatus* Chevrolat 58–209

*cubanus* Tschitschérine 03–60. (3) MX; Costa Rica, Bahamas, Cuba,  
Dominican Republic, Haiti, Puerto Rico

*floridanus* LeConte 78–376. (2) FL, AL, MS, LA; (3) TX; Bimini

*nocticolor* Darlington 34–91. Cuba

*crenatus* LeConte 52–252. (2) GA, FL, AL, MS, LA; Cuba

#### SUPERTRIBE Panagaeitae

##### TRIBE Panagaeini

#### **Coptia** Brullé 35b–433

*effeminata* Darlington 34–89. Cuba

*saurocollis* Darlington 34–88. Cuba

#### **Panagaeus** Latreille 04–291

*Hologaeus* Ogueta 66–5

*fasciatus* Say 25–70. (1) ON, NY, IN, PA, DE; (2) VA, SC, GA, FL; (5) KS;  
? Puerto Rico

*asuai* Ogueta 66–8. Dominican Republic

*quadrisingnatus* Chevrolat 35–187. (3) MX; Cuba, Puerto Rico, St. Thomas

#### SUPERTRIBE Callistitae

##### TRIBE Callistini

#### **Chlaenius** Bonelli 10–syn. tab.

*Pseudanomoglossus* Bell 60–101

*Eurydactylus* Laferté-Sénéctère 51–255

*Glyptoderus* Laferté-Sénéctère 51–260

*Anomoglossus* Chaudoir 56–192

*Agostenus* Motschulsky 50–tab. 9

*Pelasmus* Motschulsky 50–tab. 9

*Brachylobus* Chaudoir 76a–287

*Chlaeniellus* Reitter 08–185

*Merochlaenius* Grundmann 55–280

*Pachychlaenius* Grundmann 55–282

*Chlaeniopus* Grundmann 55–284

*Sericochlaenius* Grundmann 55–286

*Aulacosomus* Grundmann 55–276

*maxillosus* Horn 76–260. (2) GA, FL, AL; Bahamas

*niger* Randall 38–34. (1) NF, NS, QU, ON, WI, MI, NY, NH, MA, IL, IN,  
PA, NJ; (2) TN, SC, FL, AR, AL, LA; (3) TX; (4) WA, BC; (5) NW,  
AB, MB, MN, IA, KS; Cuba

*exaratus* Laferté-Sénéctère 51–249

*ludovicianus* Leng 15–592

*perplexus* Dejean 31–655. (2) GA, FL, AL, LA; (3) TX, MX; Cuba,  
Puerto Rico, Haiti, Dominican Republic

- circumcinctus* Say 34–418  
*virens* Chaudoir 43–753  
*poeyi* Chevrolat 63–194  
*cubanus* Chaudoir 76a–238. Cuba  
*gundlachi* Chaudoir 76a–148. Cuba  
*jamaicae* Darlington 35b–201. Jamaica  
*floridanus* Horn 76–263. (2) GA, FL; Bahamas

### TRIBE Oodini

#### **Oodes** Bonelli 10–syn. tab.

- Lachnocrepis* LeConte 53–391  
*amaroides* Dejean 31–674. Cuba, USA

#### **Stenocrepis** Chaudoir 57–39

- Stenous* Chaudoir 57–39  
*Crossocrepis* Chaudoir 57–48  
*duodecimstriata* Chevrolat 35–173. (2) SC; (3) MX; Guatemala,  
 Nicaragua, Cuba  
*gilvipes* Chaudoir 82b–504. Cuba, S. Am.  
*pallipes* Reiche 43–38  
*insulana* Jacquelin du Val 56–20. Cuba  
*metallica* Dejean 26–379. Cuba, Puerto Rico, S. Am.  
*agilis* Laferté-Sénéctère 51–273  
*palustris* Darlington 35b–202. Jamaica  
*subdepressa* Darlington 34–101. Haiti  
*tibialis* Chevrolat 34b–46. (3) MX; Guatemala, Cuba, Puerto Rico, S. Am.  
*femoralis* Chaudoir 35–444  
*pallipes* Brullé 38–32  
*sulcata* Chevrolat (Leng & Mutchler, 14–395). Cuba

#### **Anatrichis** LeConte 53–391

- Oodinus* Motschulsky 64–352  
*Oodiellus* Chaudoir 82a–322  
*piceus* Motschulsky 64–353. (2) FL; (3) TX, MX; Guatemala, Panamá,  
 Cuba S. Am.  
*mexicanus* Chaudoir 82a–323

### TRIBE Licinini

#### **Diplocheila** Brullé 34a–407

- Rembus* Dejean 26–380  
*Isorembus* Jeannel 49–771  
*major* LeConte 48–418. (1) ON, WI, MI NY, CT, RI, IN, OH, PA; (2) FL, AL,  
 LA; (3) TX; (5) SD, MN, NK, IA, KS, MO; Cuba  
*expansa* Casey 13–148  
*oblonga* Casey 13–148  
*procera* Casey 20b–200

s. *melissisa* Ball 59–78. (2) FL, AL, LA; (3) TX; Cuba

**SUPERTRIBE Harpalitae**

**TRIBE Harpalini**

**Bradycellus** Erichson 37–64

*Liocellus* Motschulsky 64–207

*Glycerius* Casey 84b–79

*Tetraplatypus* Tschitschérine 97–62

*Catharellus* Casey 14b–242

*Stenocellus* Casey 14b–243

*Liocellus* Tschitschérine 01–247

*Triliarthrus* Casey 14b–220

*festinans* Casey 14b–257. (3) TX; (5) KS, Cuba

*cubanus* Darlington 34–110. Cuba

*selleanus* Darlington 35b–204. Haiti

*velatus* Darlington 34–111. Cuba, Puerto Rico

**Acupalpus** Latreille 29–291

*Philodes* LeConte 61–33

*Goniolophus* Casey 14b–262

*Tachistodes* Casey 14b–286

*Anthracus* Motschulsky 64–207

*Aepus* LeConte 48–413

*convexus* Darlington 34–112. Cuba

*iridens* Motschulsky 64–201. Cuba

**Stenolophus** Stephens 27–67

*Agonoderus* Dejean 29–49

*Agonoleptus* Casey 14b–284

*infuscatus* Dejean 29–54. (1) NY, DE; (2) NC, SC, FL; (3) TX; Cuba

*ochropezus* Say 25–54. BJ, CA, Cuba, Puerto Rico

*convexicollis* LeConte 48–309

*gracilis* Casey 84a–14

**Pogonodaptus** Horn 81–178

*rostratus* Darlington 35b–204. Haiti

**Harpalus** Latreille 02–325

*Ophonus* Stephens 27–67

*Pheuginus* Motschulsky 45–197

*Pseudophonus* Motschulsky 45–196

*Amblystus* Motschulsky 64–209

*Pardileus* Gozis 82–289

*Ephiharpalus* Reitter 00–75

*Lasioharpalus* Reitter 00–75

*Megapangus* Casey 14b–71

*Plectralidus* Casey 14b–72

*Pharalus* Casey 14b–63

*Harpalomerus* Casey 14b–76

*Glanodes* Casey 14b–50

*Opadius* Casey 14b–63

*Eupharpalops* Casey 24–116

*Cordoharpalus* Hatch 49b–87

*Euharpalus* Hatch 53–170

integer Fabricius 01–196. Guadeloupe, Hispaniola

*grimmi* Sturm 26–148

**Selenophorus** Dejean 29–80

*Selenalius* Casey 14b–253

*Hemisopalus* Casey 14b–135

*Celiomorphus* Casey 14b–141

*Gynandropus* Dejean 31–817

alternans Dejean 29–86. (3) MX; Cuba Hispaniola, Puerto Rico,

Guadeloupe, S. Am.

*lineatopunctatus* Dejean 29–86

beauvoisi Dejean 29–98. Jamaica, Puerto Rico

*aneocupreus* Dejean 29–99

cariniger Putzeys 78a–44. Hispaniola

chalybaeus Dejean 29–110. Bahamas, Cuba, Is. Pinos, Jamaica, Hispaniola,

Puerto Rico, Antigua, Guadeloupe

cinctus Putzeys 78a–45. Cuba

cyaneopacus Darlington 34–107. Haiti

discopunctatus Dejean 29–92. (2) FL; Cuba, Is Pinos, Hispaniola, Puerto Rico,

Antigua, S. Am.

*chokoloskei* Leng 15–596

*aeratus* Reiche 43–142

*cuprinus* Dejean 29–96

*harpaloides* Reiche 43–142

dubius Putzeys 78a–54. West Indies

flavilabris Dejean 29–97. Cuba, Puerto Rico

s. cubanus Darlington 35b–203. Cuba

guadeloupensis Fleutiaux & Sallé 89–365. Puerto Rico, Guadeloupe

haitianus Darlington 34–107. Haiti

laticus Darlington 34–109. Dominican Republic, Puerto Rico

lucidulus Dejean 29–85. West Indies

macleayi Kirby 37–50. West Indies

mundus Putzeys 78a–29. (3) MX; West Indies

nonseriatus Darlington 34–109. Jamaica, Dominican Republic

parumpunctatus Dejean 29–104. West Indies

parvus Darlington 34–105. Puerto Rico

propinquus Putzeys 74–118. Antigua, Guadeloupe

pubifer Putzeys 78a–69. West Indies, S. Am.

*puberulus* Putzeys 74–119

puertoricensis Mutchler 34a–5. Puerto Rico

puncticollis Putzeys 78a–34. Dominican Republic

pyritosus Dejean 29–84. (3) MX; Guatemala, Honduras, Nicaragua, Panamá,



Cuba, Is. Pinos, Puerto Rico

*ramosi* Darlington 29–97. Puerto Rico

*sinuatus* Gyllenhal 06–203. Cuba, Puerto Rico, Antigua, Guadeloupe

*solitarius* Darlington 34–106. Cuba

*striatopunctatus* Putzeys 78a–33. (3) MX; Cuba, Puerto Rico

*subaeneus* Reiche 43–141. Panamá, Guadeloupe, S. Am.

*subquadratus* Putzeys 78b–293. Cuba, Hispaniola

*thoracicus* Putzeys 78a–59. Haiti

*excisus* Putzeys 78a–59

**Amblygnathus** Dejean 29–62

*vitraci* Fleutiaux & Sallé 89–364. Guadeloupe, Dominica

*puncticollis* Putzeys 78a–34. Dominican Republic

*guadeloupensis* Fleutiaux & Sallé 89–365. Puerto Rico, Guadeloupe

**Athrostictus** Bates 78–592

*iridescens* Chaudoir 43–783. Guadeloupe

**Stenomorphus** Dejean 31–696

*Agaosoma* Ménétriés 44–63

*manni* Darlington 34–102. Haiti

*cubanus* Darlington 37a–135. Cuba

SUPERTRIBE Dryptitae

TRIBE Zuphiini

**Pseudaptinus** Laporte 35–56

*Diaphorus* Dejean 31–300

*cubanus* Chaudoir 77–252. (2) FL; Cuba

*deceptor* Darlington 34–128. Cuba

*insularis* Mutchler 34a–4. Cuba, Puerto Rico

*salebrosus* Liebke 34–375. Cuba

*thaxteri* Darlington 34–127. Grenada

**Thalpius** LeConte 51–174

*Enaphorus* LeConte 51–174

*Zuphiosoma* Laporte 67–103

*apicalis* Darlington 34–125. Cuba

*arrogans* Liebke 34–385. Cuba

*bierigi* Liebke 34–387. Cuba

*dorsalis* Brullé 34a–181. Cuba

*marginicollis* Darlington 34–126. Cuba

*s. fumipes* Darlington 35b–212. Haiti

*pygmaeus* Dejean 26–460. (2) FL, LA; Cuba

**Zophium** Latreille 06–198

*Zophium* Gistel 38–112

*Zoyphium* Motschulsky 50–t. 8

*americanum* Dejean 31–298. (1) ON, MI; (2) LA, SC; (3) TX; (4) OR;

(5) SD, KS; Puerto Rico

*bierigi* Liebke 33–467. Cuba

cubanum Liebke 33–470. Cuba  
 haitianum Darlington 35b–213. Haiti  
 mexicanum Chaudoir 62–314. Cuba

# TRIBE Galeritini

## Galerita Fabricius 01–214

*Galeritula* Strand 36–168  
*Progaleritina* Jeannel 49–1058  
*Diabena* Fairmaire 01–94  
*Galeritiola* Jeannel 49–1059  
*Galericeps* Jeannel 49–1058  
*Galeritella* Jeannel 49–1058  
*lecontei* Dejean 31–294. USA; (3) MX.  
*s. tenebricosa* Klug 34–65. Dominican Republic, Haiti, Cuba, Cayman Is.  
*vetula* Chevrolat 63–186.  
*ruficollis* Dejean 25–191. (3) MX, Panamá, Cuba, Jamaica  
*erthrodera* Brullé 34b–103  
*thoracica* Chevrolat 34b–34  
*humboldti* Gistel 37–11  
*insularis* Laporte 40–36  
*americana* Linné 58–415. Guatemala, Costa Rica, Panamá, S. Am., Trinidad,  
 Guadeloupe, St. Martin  
*microcostata* Darlington 34–124. Puerto Rico  
*beauvoisi* Chaudoir 61–553. Costa Rica, Haiti  
*tristis* Reiche 42–273. El Salvador, Costa Rica, Panamá, Guadeloupe, Dominica,  
 Jamaica, S. Am.  
*lugens* Chaudoir 48–65  
*melanaria* Erichson 48–555  
*unicolor* Latreille & Dejean 23–117 Cuba, S. Am.  
*porcata* Klug 34–66  
*bahiana* Liebke 39b–477  
*striata* Klug 34–66. Haiti  
*montana* Darlington 35b–211

## SUPERTRIBE Ctenodactylitae

### TRIBE Ctenodactylini

## Leptotrachelus Latreille 29–371

*Odacantha* Perty 30–2  
*Rhagocrepis* Eschscholtz 29–5  
*Sphaeracra* Say 34–412  
*dorsalis* Fabricius 01–220. (1) ON, NY, DE, DC; (2) SC, FL; (3) SC, KS; Cuba

## SUPERTRIBE Lebiitae

## TRIBE Perigonini

**Perigona** Laporte 35–151*Nestra* Motschulsky 51–506*Spathicus* Nietner 58–428*Trechicus* LeConte 53–386*nigriceps* Dejean 31–44. (1) QU, IN, NJ, NH, DC; (2) NC, SC, FL, AL;

(3) CA; Cuba, Puerto Rico, Guadeloupe, Martinique, (Old World)

*pallipennis* LeConte 53–386*umbripennis* LeConte 53–386*testaceolimbata* Motschulsky 62–33*glabrella* Motschulsky 62–34*guadeloupensis* Fleutiaux & Sallé 89–367. Guadeloupe*laevigata* Bates 72a–200. MX, C. Am., Cuba*microps* Darlington 34–99. Puerto Rico*picea* Darlington 34–98. Cuba, Haiti, Dominican Republic, Guadeloupe

## TRIBE Lachnophorini

**Anchonoderus** Reiche 43–38*subtilis* Bates 71a–33. (3) MX; Guatemala, Cuba*leucopterus* Chevrolat 63–198. Cuba, Puerto Rico**Lachnophorus** Dejean 31–28*Aretaonus* Liebke 36–461*Stigmaphorus* Motschulsky 62–48*leucopterus* Chevrolat 63–198. Cuba, Puerto Rico**Euphorticus** Horn 81–144*pubescens* Dejean 31–30. (2) NC, GA, FL, AL; (3) BJ, MX; Guatemala, S. Am.*laevicollis* Reiche 43–180*niger* Gory 33–245*s. aeneolus* Bates 83–156. (3) MX; Guatemala, Cuba, S. Am.**Eucaerus** LeConte 53–386*haitianus* Darlington 35b–210. Haiti*insularis* Darlington 34–120. Cuba

## TRIBE Cyclosomini

**Tetragonoderus** Dejean 29–485*Peronoscelis* Chaudoir 76b–29*intersectus* (Germar) 24–28 (2) KY, TN, SC, GA, FL, AL; (3) TX, MX;

Bahamas

# TRIBE Masoreini

## **Macracanthus** Chaudoir 46a–539

*Masoreus auctorum*

brevicillus (Chevrolat) 63–189. Cuba, Puerto Rico

## **Aephnidius** MacLeay 25–23

*Masoreus auctorum*

ciliatus Mutchler 34b–130. Cuba, Puerto Rico

# TRIBE Pentagonicini

## **Pentagonica** Schmidt-Goebel 46–47

*Rhombodera* Reiche 42–313

*Didetus* LeConte 53–377

nigricornis Darlington 34–121. (2) FL; Cuba

flavipes LeConte 53–377. (2) SC, FL, AR, LA, Belize, Costa Rica, Panamá,  
Jamaica, Guadeloupe, Cuba, Puerto Rico, S. Am.

s. picipes Darlington 35b–211. Jamaica, Hispaniola, Puerto Rico

*pallipes* LeConte 63–6

*americana* Motschulsky 64–224

*albipes* Bates 83–218

*picea* Fleutiaux & Sallé 89–362

divisa Darlington 34–121. Puerto Rico

*atorrufa* Gundlach 93–292

*bicolor* Leng & Mutchler 17–195

nigricornis Darlington 34–121. Cuba

vittula Darlington 39–100. Dominican Republic

# TRIBE Odacanthini

## **Colliuris** Degeer 74–79

*Anaplagiorrhytis* Liebke 30–658

*Apiodera* Chaudoir 48–35

*Apioderella* Csiki 32b–1532

*Apioderma* Csiki 32b–1523

*Calocolliuris* Csiki 32b–1522

*Casnoniella* Csiki 32b–1522

*Colliurella* Liebke 30–658

*Colliurina* Liebke 30–658

*Colliurita* Csiki 32b–1531

*Casnonia* Latreille & Dejean 22–77

*Isocasnonia* Csiki 32b–1532

*Mimocasnonia* Csiki 32b–1532

*Odacantha* Paykull 98–169

*Odacanthella* Liebke 30–658

*Odacanthina* Csiki 32b–1522

*Ophionea* Klug 21–298  
*Paracollinus* Liebke 30–653  
*Paracolluris* Liebke 30–658  
*Plagiorrhysis* Chaudoir 48–31  
*Procolluris* Liebke 30–669  
*Pseudocasonia* Liebke 30–658  
*Pseudoplagiorrhysis* Liebke 30–657

*gundlachi* Darlington 34–122. Cuba  
*limbata* Waterhouse 78–304. Jamaica  
*noah* Darlington 34–123. Cuba  
*picta* Chaudoir 43–697. (3) AZ, TX, MX  
*suturalis* Chaudoir 72a–405  
*s. concluda* Liebke 30–689. (3) MX; Cuba  
*s. extrema* Liebke 30–689. (3) MX; Cuba  
*portoricensis* Liebke 30–688. Haiti, Puerto Rico  
*rufipes* Dejean 25–172. S. Am.  
*s. insignis* Chaudoir 48–41. Puerto Rico, S. Am.  
*tetrastigma* Chaudoir 62–278. (3) MX  
*s. caymanensis* Darlington 47–211. Cayman Is.

#### TRIBE Lebiini

##### **Apenes** LeConte 51–174

*aptera* Darlington 35b–209. Jamaica  
*coriacea* Chevrolat 63–188. Cuba  
*laevicincta* Darlington 34–119. Haiti  
*lata* Darlington 34–119. Bahamas, Cuba  
*marginalis* Dejean 31–315. Puerto Rico, Guadeloupe, Dominica, S. Am.  
*ovalis* Darlington 35b–210. Haiti  
*pallipes* Fabricius 92–159. Puerto Rico, Antigua, Guadeloupe  
*guadeloupensis* Gory 33–186  
*variegata* Dejean 25–217  
*parallela* Dejean 25–218. (3) MX; Bahamas, Cuba, Puerto Rico  
*s. inaguae* Darlington 53–14. Bahamas  
*delicata* Darlington 34–118. Cuba  
*portoricensis* Darlington 39–100. Puerto Rico  
*purpurata* Fleutiaux & Sallé 89–360. Guadeloupe  
*strandi* Liebke 39a–119. Cuba  
*sulcicollis* Jacquelin du Val 57–8. Cuba  
*opaca* LeConte 51–175. Bahamas, USA

##### **Apristus** Chaudoir 46b–12

*sericeus* Darlington 34–116. Cuba

##### **Microlestes** Schmidt-Goebel 46–41

*Blechrus* Motschulsky 47–219  
*Bomius* LeConte 51–177  
*Dromius* Sloane 98–494

poeyi Jacquelin du Val 57–10. Cuba

**Somotrichus** Seidlitz 87–7

unifasciatus Dejean 31–389. (4) WA; Cosmop., Guadeloupe

*elevatus* Fabricius 87–198

*bicinctus* Hope 45–15

*massiliensis* Fairmaire 49–419

**Phloeoxena** Chaudoir 69–145

*Tacana* Ball 75–182

*Oenaphelox* Ball 75–205

costata Darlington 37a–135. Cuba

dealata Darlington 37a–136. Cuba

montana Darlington 35b–208. Hispaniola

plagiata Darlington 34–114. Cuba

imitatrix Darlington 34–114. Cuba

schwarzi Darlington 34–115. Cuba

portoricensis Darlington 39–99. Puerto Rico

**Coptodera** Dejean 25–173

festiva Dejean 25–174. Cuba, Jamaica

unicolor Chevrolat 34b–40. (3) MX; Guatemala, Nicaragua, Panamá, Cuba

*obscura* Laporte 35–51

**Galerucidia** Chaudoir 72a–416

dimidiata Chaudoir 72a–420. Cuba

**Calleida** Dejean 25–220

*Callida auctorum*

*Philophuga* Motschulsky 59–140

rubricollis Dejean 25–225. Cuba; “? USA”

*elegans* Chaudoir 44–469

caymanensis Darlington 47–210. Cayman Is.

bahamensis Darlington 53–11. Bimini

decolor Chaudoir 72b–131. Martinique

pretiosa Chaudoir 72b–124. Hispaniola

tinctula Darlington 34–117. Cuba

**Euproctinus** Leng & Mutchler 27–14

*Euproctus* Solier 49–131

*Andrewesella* Csiki 32b–1456

trivittatus LeConte 78–373. (2) FL; Cuba

**Plochionus** Latreille & Dejean 24–150

*Menidius* Chaudoir 72b–170

pallens Fabricius 75–244. (1) MA, PA; (2) FL; MX, C. Am., S. Am., Cuba,

Bahamas Is., Old World

bicolor Notman 19–234. (2) FL; Cuba

**Lebia** Latreille 02–85

*Chelonodema* Laporte 35–49

*Lia* Eschscholtz 29–7

*Loxopeza* Chaudoir 70–138

*Polycheloma* Madge 67–163

- Lamprias* Bonelli 10—syn. tab.  
*Echimuthus* Leach 15–81  
*Omalomorpha* Motschulsky 45–42  
*Homalops* Motschulsky 50–42  
*Lebida* Motschulsky 62–51  
*Metabola* Chaudoir 70–160  
*Aphelogenia* Chaudoir 71a–25  
*Dianchomena* Chaudoir 71a–45  
*frenata* Chaudoir 71a–27. S. Am.  
*s. chevrolati* Blackwelder 44–54. Guadeloupe  
*apicalis* Fleutiaux & Sallé 89–361  
*gibba* Darlington 35b–207. Haiti  
*nigrita* Darlington 35b–206. Haiti  
*nubicola* Darlington 39–98. Dominican Republic  
*tericola* Darlington 39–98. Dominican Republic

## APPENDIX B: CURRENT REVISORS OF WEST INDIAN GENERA

G. E. Ball

Department of Entomology

University of Alberta

Edmonton, Alberta

Canada T6G 2E3

R. T. Bell

Department of Zoology

Marsh Life Science Building

The University of Vermont

Burlington, Vermont

U.S.A. 05405

R. Davidson

Section of Entomology

Carnegie Museum of Natural History

4400 Forbes Avenue

Pittsburgh, Pennsylvania

U.S.A. 15213

T. L. Erwin

Department of Entomology

National Museum of Natural History

Smithsonian Institution

Washington, D.C.

U.S.A. 20560

R. Freitag

Department of Biology

Lakehead University

Thunder Bay, Ontario

Canada P7B 5E1

M. A. Ivie

Department of Entomology

1735 Neil Avenue

Ohio State University

Columbus, Ohio

U.S.A. 43210



D. H. Kavanaugh  
Department of Entomology  
California Academy of Sciences  
Golden Gate Park  
San Francisco, California  
U.S.A. 94118

J. K. Liebherr  
Department of Entomology  
Cornell University  
Ithaca, New York  
U.S.A. 14853

D. R. Maddison  
Department of Entomology  
University of Alberta  
Edmonton, Alberta  
Canada T6G 2E3

J. Mateu  
Faculte des Sciences de Paris  
Laboratoire d'Evolution des Etres Organises  
105, Boulevard Raspail  
Paris (VI)e, France

R. R. Murray  
Department of Invertebrate Zoology  
Milwaukee Public Museum  
800 West Wells Street  
Milwaukee, Wisconsin  
U.S.A. 53233

G. R. Noonan  
Department of Invertebrate Zoology  
Milwaukee Public Museum  
800 West Wells Street  
Milwaukee, Wisconsin  
U.S.A. 53233

L. L. Sims  
Department of Entomology  
National Museum of Natural History  
Smithsonian Institution  
Washington, D. C.  
U.S.A. 20560

J. R. Spence  
Department of Entomology  
University of Alberta  
Edmonton, Alberta  
Canada T6G 2E3

N. E. Stork  
British Museum (Natural History)  
Department of Entomology  
Cromwell Road  
London S.W. 7, England

Shun-ichi Ueno  
Department of Zoology  
The National Science Museum  
Ueno Park  
Tokyo, Japan

## INDEX TO NAMES OF TAXA

(Synonyms in italics)

## FAMILY GROUP TAXA

- Agonicini, 356  
 Agonina, 361, 364, 382–383, 397  
 Agonini, 382–383, 393  
 Agridae, 422  
 Amarotypini, 355  
 Amblystomi, 389  
 Amblytelini, 356  
 Amorphomerini, 356  
*Anaulacini*, 394  
 Anchomenidae, 422  
*Anchomenina*, 383  
 Anchonoderinae, 393  
 Anchonoderini, 393  
 Anillina, 378  
 Anthiadae, 422  
 Anthiini, 356  
 Anthiitae, 356  
 Apenina, 397  
 Aplothoracina, 365  
 Apotomidae, 422  
 Apotomini, 355, 359  
 Apotomitae, 355  
 Aptinina, 375  
*Ardistomina*, 369, 371  
 Attini, 374  
 Bascanini, 356  
 Bembidiidae, 422  
 Bembidiina, 378, 381  
 Bembidiini, 352, 356, 377–378, 429  
 Brachinidae, 373–374, 422  
 Brachinina, 375  
 Brachininae, 369  
 Brachinini, 352, 355, 357, 364, 375, 428  
 Brachinitae, 355, 374–375, 428  
*Bradycellina*, 388  
 Broschidae, 422  
 Broscinae, 355  
 Broscini, 355, 359  
 Broscitae, 355  
 Caelostomina, 383–384  
 Calleidina, 396–399  
*Callidina*, 398  
 Callistidae, 422  
 Callistinae, 386  
 Callistini, 352, 356, 361, 386, 437  
 Callistitae, 356, 386, 437  
 Calophaenini, 357  
 Calosomina, 365  
 Calpohaenidae, 422  
 Camptonotini, 373  
 Carabidae, 352, 354, 357, 364, 366, 373, 376, 382, 386, 399  
 Carabina, 365  
 Carabinae, 354, 364, 422  
 Carabini, 352, 354, 359, 364–365, 422  
 Carabitae, 354, 364, 366, 422  
 Caraboidea, 354  
 Caraboidea Limbata, 364  
 Caraboidea Simplicia, 364  
 Catapiesi, 382  
 Catapiesini, 356, 361  
*Catascopina*, 397  
 Ceroglossina, 365  
 Ceroglossini, 354  
 Chaetogenyini, 356, 361  
 Chlaeniidae, 422  
 Chlaeniini, 386  
 Chrysomelidae, 396  
 Cicindelinae, 366  
 Cicindelini, 352, 354, 358, 366, 424  
 Cicindelitae, 354, 357, 366, 376, 423  
 Cicindisini, 354, 358  
 Clivinina, 369, 371–372  
 Clivinini, 352, 355, 369–371, 373, 426  
 Cnemacanthidae, 422  
 Cnemacanthini, 355, 360  
 Colliurini, 393, 395  
 Collyrinae, 366  
 Collyrini, 354  
 Colydiidae, 376, 378  
*Coptoderina*, 397  
*Cratocarina*, 388  
 Crepidogastrini, 355, 374  
 Ctenodactylidae, 422  
 Ctenodactylini, 352, 357, 362, 392, 395, 442  
 Ctenodactylitae, 356, 392, 442

- Ctenostomatini, 354, 357, 366  
 Ctenostomini, 366  
 Cuneiptectini, 356  
 Cychrina, 365  
 Cychrini, 354, 359  
 Cyclosomidae, 422  
 Cyclosomini, 352, 357, 362, 394, 443  
 Cymbionotidae, 422  
 Cymbionotini, 355  
 Cymindina, 396  
 Disphaericini, 356  
 Dolichoderini, 374  
 Dromiina, 397  
 Dryptidae, 422  
 Dryptini, 356, 362, 390–391  
 Dryptitae, 356, 390, 441  
 Dyschiriina, 369, 371  
 Elaphridae, 422  
 Elaphrini, 355  
 Elaphritae, 355  
 Enceladini, 352, 355, 359, 368, 425  
 Euchelini, 396  
 Euchroina, 383–384  
 Feronidae, 422  
 Forcipatorina, 369, 371, 373  
 Galeritini, 352, 356, 390–392, 442  
*Galerudiciina*, 398  
 Gehringiidae, 422  
 Gehringiini, 355  
 Glyptidae, 422  
 Graphipterini, 357  
 Harpalidae, 422  
 Harpalina, 388–389  
 Harpalinae, 356, 364, 368, 381, 432  
*Harpalinae Impilae*, 364  
*Harpalinae Piliiferae*, 364  
 Harpalini, 352, 356, 388, 439  
 Harpalitae, 356, 388, 439  
 Helluodini, 356  
 Helluonini, 352, 356, 363, 390  
 Hexagoniini, 356  
 Hiletidae, 422  
 Hiletini, 355, 358  
 Hiletitae, 355  
 Hydrophilidae, 375  
 Hymenoptera, 372  
 Idiomorphini, 356  
 Lachnophorinae, 393  
 Lachnophorini, 352, 357, 363–364, 383, 392–393, 443  
 Lebiidiina, 397–398  
 Lebiidae, 422  
 Lebiina, 399  
 Lebiini, 352, 357, 362–363, 388, 395–398, 445  
 Lebiitae, 357, 382, 392–393, 442  
 Leleupidiina, 391  
 Licindae, 422  
 Licinini, 352, 356, 363, 387, 438  
 Limnastina, 379  
 Loricerini, 354, 359  
 Loriceritae, 354  
 Loroceridae, 422  
 Loxandrina, 383, 385  
 Mantichorini, 354, 366  
 Masoreidae, 422  
 Masoreini, 352, 357, 363, 394, 396, 444  
 Mastacina, 375  
 Megacephalini, 352, 354, 358, 366, 423  
 Melaenini, 355  
 Melaenitae, 355  
 Melanodidae, 422  
 Melisoderi, 382  
 Melisoderini, 356  
 Meonidi, 382  
 Meonidini, 356  
 Metriidae, 422  
 Metriini, 355  
 Metriitae, 355, 373  
 Micratopina, 379  
 Migadopidae, 422  
 Migadopini, 355, 359  
 Migadopitae, 355  
 Morionini, 352, 356, 362, 369, 376, 381–382, 432  
 Mormolycini, 396–397  
 Myrmicini, 373  
 Mystropomini, 355  
 Nebriidae, 422  
 Nebriiformes, 354  
 Nebriini, 354  
 Nebriitae, 354

- Noctuidae, 396  
 Nomiini, 382  
 Notiokasini, 354  
 Notiophilini, 354, 359  
 Nototylini, 355, 358, 373  
 Odacanthidae, 422  
 Odacanthini, 352, 357, 362, 392, 395, 444  
 Omophronidae, 422  
 Omophronini, 354, 357, 367, 376  
 Omophronitae, 354, 367  
 Omphreinae, 393  
 Oodina, 386  
 Oodini, 352, 356, 361, 386–387, 438  
 Opisthiini, 354  
 Orthogoniidae, 422  
 Orthogoniini, 356  
 Orthogoniitae, 356  
*Oxystomina*, 373  
 Ozaenidae, 422  
 Ozaeninae, 373  
 Ozaenini, 352, 355, 358, 373–374, 427  
 Pamborini, 354  
 Panagaeidae, 422  
 Panagaeini, 352, 356, 360, 385, 437  
 Panagaeitae, 356, 385, 437  
 Patriziina, 391  
 Patrobidae, 422  
 Patrobini, 356  
 Paussidae, 373, 422  
 Paussinae, 355, 373, 376, 427  
 Paussini, 355, 358, 373  
 Paussitae, 355, 358, 373, 375, 427  
 Peleciidae, 422  
 Peleciini, 356, 361  
 Pentagonicidae, 422  
 Pentagonicini, 352, 357, 363, 395, 444  
 Pericalidae, 422  
 Pericalina, 363, 396–398  
 Perigonidae, 422  
 Perigonini, 352, 357, 364, 393, 442  
 Perileptina, 377  
 Pheropsophina, 375  
*Platynina*, 383  
 Pogonini, 352, 356, 360, 377, 429  
 Polyphaga, 376  
 Promecognathini, 355  
 Promecognathitae, 355  
 Protopaussini, 355, 373  
 Pseudomorphidae, 422  
 Pseudomorphini, 352, 355, 357, 368–369, 425  
 Pseudomorphitae, 355, 368, 425  
 Psydri, 382  
 Psydridae, 422  
 Psydrinae, 355, 376, 428  
 Psydrini, 355, 360, 382  
 Psydritae, 355  
 Pterostichidae, 422  
 Pterostichina, 382–384  
 Pterostichini, 352, 356, 361–362, 364, 376, 381–384, 388, 393, 397, 432  
 Pterostichitae, 356, 381, 432  
 Pyralidae, 396  
 Rhysodini, 352, 356, 358, 376, 428  
 Rhysoditae, 356, 376, 428  
 Salcediina, 373, 376  
 Scapterina, 370  
 Scaritidae, 422  
 Scaritina, 369–370  
 Scaritinae, 355, 364, 368, 425  
 Scaritini, 352, 355, 369–370, 376, 425  
 Scarititae, 355, 359, 369, 376, 425  
 Selenophori, 389–390  
 Siagonidae, 422  
 Siagonini, 355  
 Siagonitae, 355, 368, 425  
 Sigonitae, 368  
 Sphodrina, 383  
 Stenolophina, 388  
 Systolosomini, 354, 358  
 Tachyina, 378–379  
*Tetragonoderini*, 394  
 Thyreopteridae, 422  
*Thyreopterina*, 397  
 Trachypachidae, 354, 358  
 Trachypachini, 354  
 Trechidae, 422  
 Trechini, 352, 356, 360, 377, 429  
 Trechitae, 356, 377, 429  
 Tropidoptera, 382  
 Tropidopterini, 356  
 Zabrinini, 356, 362

Zolini, 356, 360  
 Zuphiidae, 422  
 Zuphiina, 391  
 Zuphiini, 352, 356, 363, 390–391, 441

#### GENERA AND SUBGENERA

- Acamegonia* Lapouge, 422  
*Acampalita* Lapouge, 422  
*Actedium* Motschulsky, 431  
*Actenonyx* White, 395  
*Acupalpus* Latreille, 388–389, 439  
*Acupalpus* Thomson, 389  
*Adialampus* Gozis, 370  
*Aephnidius* MacLeay, 394–395, 444  
*Aepus* LeConte, 439  
*Agaosoma* Ménétériés, 390, 441  
*Agonoderus* Dejean, 439  
*Agonoleptus* Casey, 439  
*Agonum* (*sensu stricto*), 384  
*Agonum* Bonelli, 383–384, 432  
*Agostenus* Motschulsky, 437  
*Agra* Fabricius, 362, 374, 395–396  
*Akephorus* LeConte, 371, 426  
*Alkestis* Csiki, 399  
*Allotriopus* Bates, 436  
*Amara* Bonelli, 362  
*Amblygnathus* Dejean, 389, 441  
*Amblystus* Motschulsky, 439  
*Americomaseus* Csiki, 436  
*Amerizus* Chaudoir, 431  
*Ameroglymmius* Bell & Bell, 428  
*Anacolpodes* Casey, 433  
*Anaplagiorrhysis* Liebke, 444  
*Anatrichis* (*sensu stricto*), 387  
*Anatrichis* LeConte, 387, 438  
*Anaulacus* MacLeay, 395  
*Anchomenus auctorum*, 432–433  
*Anchomenus* Bonelli, 384  
*Anchomenus* Samouelle, 432  
*Anchonoderus* Reiche, 394, 443  
*Anchus* LeConte, 433  
*Andrewesella* Csiki, 399, 446  
*Anilloferonia* Van Dyke, 436  
*Anisotarsus* Dejean, 388  
*Anomoglossus* Chaudoir, 437  
*Anthracus* Motschulsky, 439  
*Antilliscaris* Bänninger, 370–371, 425  
*Apenes* LeConte, 396–397, 445  
*Aphelogenia* Chaudoir, 447  
*Apiodera* Chaudoir, 444  
*Apioderella* Csiki, 444  
*Apioderma* Csiki, 444  
*Apotomus* Illiger, 359  
*Apristus* Chaudoir, 397, 445  
*Archicarabus* Seidlitz, 423  
*Arctoclinidium* Bell, 428  
*Ardistomiellus* Kult, 373, 427  
*Ardistomis* (*sensu stricto*), 371, 373  
*Ardistomis* Kult, 373  
*Ardistomis* Putzeys, 371–373, 427  
*Aretaonus* Liebke, 443  
*Argutor* Stephens, 436  
*Argyrobracteon* Netolitzky, 431  
*Arthrostictus auctorum*, 390  
*Aspasiola* Csiki, 399  
*Aspidoglossa* Putzeys, 371–373, 427  
*Athrostictus* Bates, 389–390, 441  
*Aulacopterus* Gehin, 423  
*Aulacosomus* Grundmann, 386, 437  
*Aureoplataphus* Netolitzky, 431  
*Autocarabus* Seidlitz, 423  
*Axinophorus* Dejean & Boisduval, 369, 425  
*Badister* Clairville, 387  
*Barytachys* Chaudoir, 380, 429  
*Bembidion* Latreille, 377–378, 381, 430  
*Bembidionetolitzkya* Strand, 431  
*Bembidium auctorum*, 381  
*Blaptosoma* Gehin, 422  
*Blechrus* Motschulsky, 397, 445  
*Blemus* LeConte, 381, 430  
*Blepharoplataphus* Netolitzky, 431  
*Bomius* LeConte, 397, 445  
*Boreobia* Tschitschérine, 436  
*Bothriopterus* Chaudoir, 435  
*Brachinus* Erwin, 375  
*Brachinus* Weber, 375, 428  
*Brachylobus* Chaudoir, 437  
*Brachynus auctorum*, 375, 428  
*Brachystilus* Chaudoir, 435  
*Bracteomimus* Lindroth, 431

- Bracteon* Bedel, 430  
*Bradycellus* Erichson, 389, 439  
*Brasiella* Rivalier, 367  
*Caelostomus* MacLeay, 383–384, 436  
*Calamata* Motschulsky, 422  
*Calleida* Dejean, 395–396, 399, 446  
*Callida auctorum*, 399, 446  
*Callipara* Motschulsky, 422  
*Callistenia* Lapouge, 423  
*Callisthenes* Fischer von Waldheim, 423  
*Callistriga* Motschulsky, 422  
*Callitropa* Motschulsky, 422  
*Calocolliuris* Csiki, 444  
*Calodrepa* Motschulsky, 422  
*Calopachys* Haury, 423  
*Calosoma* Weber, 365, 422  
*Camedula* Motschulsky, 422  
*Camegonia* Lapouge, 422  
*Camptotoma* Reiche, 361  
*Carabomimus* Kolbe, 423  
*Carabosoma* Gehin, 422  
*Carabus* Linné, 365, 423  
*Casnonia* Latreille & Dejean, 395, 444  
*Casnoniella* Csiki, 444  
*Castrida* Motschulsky, 422  
*Catastriga* Lapouge, 422  
*Catharellus* Casey, 439  
*Celiamorphus* Casey, 390, 440  
*Ceratoglossa* MacLeay, 372  
*Ceroglossus* Solier, 365  
*Chaenius* Bonelli, 386  
*Chelonodema* Laporte, 396, 446  
*Chinocillenus* Netolitzky, 431  
*Chlaeniellus* Reitter, 437  
*Chlaeniopus*, 437  
*Chlaenius (sensu stricto)*, 386  
*Chlaenius* Bonelli, 386, 437  
*Chrysobracteon* Netolitzky, 430  
*Chrysostigma* Kirby, 422  
*Cicindela* Linné, 366, 424  
*Cicindela sensu lato*, 367  
*Cicindelidia* Rivalier, 367  
*Cicindis* Bruch, 358  
*Circinalia* Casey, 432  
*Circinalidia* Casey, 432  
*Clinidium (sensu stricto)*, 376  
*Clinidium* Kirby, 376, 428  
*Clinidium* Kirby, 376  
*Clivina (sensu stricto)*, 372  
*Clivina* Latreille, 372, 426  
*Cnemalobus* Guérin-Mèneville, 360  
*Colleida* Dejean, 399  
*Colliurella* Liebke, 444  
*Colliurina* Liebke, 444  
*Colliuris* Degeer, 395, 444  
*Colliurita* Csiki, 444  
*Colpodes auctorum*, 382, 384, 433  
*Comstockia* Van Dyke, 433  
*Conicibracteon* Netolitzky, 431  
*Coptia* Brullé, 385, 437  
*Coptodera* Dejean, 397–398, 446  
*Cordoharpalus* Hatch, 440  
*Costitachys* Erwin, 379  
*Cratocerus* Dejean, 361, 382  
*Crossocrepis* Chaudoir, 387, 438  
*Cryobius* Chaudoir, 436  
*Cryocarabus* Lapouge, 423  
*Cryptobatis* Csiki, 399  
*Ctenostoma* Klug, 357  
*Cyclolopha* Casey, 431  
*Cylindera (sensu stricto)*, 367  
*Cylindera* Westwood, 367  
*Cylindrobacteon* Netolitzky, 431  
*Cylindrocharis* Casey, 435  
*Cyrtolaus* Bates, 361  
*Dailodontus* Reiche, 390  
*Daniela* Netolitzky, 431  
*Deratanchus* Casey, 432  
*Derulus* Tschitschérine, 435  
*Derus* Motschulsky, 435  
*Desarmatocillenus* Netolitzky, 431  
*Diabena* Fairmaire, 442  
*Dianchomena* Chaudoir, 447  
*Diaphorus* Dejean, 391, 441  
*Dicaelus* Bonelli, 387  
*Didetus* LeConte, 395, 444  
*Diocarabus* Reitter, 423  
*Diplocampa* Bedel, 431  
*Diplochaetus* Chaudoir, 377, 429  
*Diplocheila* Brullé, 387–388, 438  
*Dischistus* Portevin, 370

- Distichus* Motschulsky, 370  
*Drepanus* Dejean, 369, 425  
*Dromius* Sloane, 397, 445  
*Dromochorus* Guérin-Ménéville, 367  
*Dyschiridius* Jeannel, 371, 426  
*Dyschirius* Bonelli, 369, 371, 426  
*Dyschromus* Chaudoir, 383–384, 435  
*Dyscolus* Dejean, 433  
*Dysidius* Chaudoir, 435  
*Echimuthus* Leach, 447  
*Eidocompsus* Erwin, 380, 429  
*Elaphropus* Motschulsky, 379–380, 429  
*Ellipsoptera* Dokhtouroff, 367  
*Enaphorus* LeConte, 391, 441  
*Enceladus* Bonelli, 368, 425  
*Eotachys* Jeannel, 381, 430  
*Ephiharpalus* Reitter, 439  
*Eucaerus* LeConte, 363, 393–394, 443  
*Eucamaragnathus* Jeannel, 358  
*Eucarabus* Gehin, 423  
*Eudromus* Kirby, 431  
*Euferonia* Casey, 435  
*Euharpalus* Hatch, 440  
*Eunota* Rivalier, 367  
*Eupalamus* Schmidt-Goebel, 372, 426  
*Eupetedromus* Netolitzky, 431  
*Eupharpalops* Casey, 440  
*Euphorticus* Horn, 394, 443  
*Euproctinus* Leng & Mutchler, 396, 399, 446  
*Euproctus* Solier, 399, 446  
*Europhilus* Chaudoir, 433  
*Eurycoleus* Chaudoir, 398  
*Eurydactylus* Laferté-Sénéctère, 386, 437  
*Euryderus* LeConte, 390  
*Euryperis* Motschulsky, 436  
*Eurytrachelus* Motschulsky, 431  
*Eutelodontum* Gehin, 423  
*Eutogeneius* Solier, 387  
*Feronia* Latreille, 435  
*Feronina* Casey, 436  
*Foveobracteon* Netolitzky, 431  
*Furcacampa* Netolitzky, 431  
*Galericeps* Jeannel, 442  
*Galerita* Fabricius, 374, 392, 442  
*Galeritella* Jeannel, 442  
*Galeritiola* Jeannel, 442  
*Galeritula* Strand, 442  
*Galerucidia* Chaudoir, 398, 446  
*Gastrellarius* Casey, 435  
*Gastrosticta* Casey, 436  
*Genioschizus* Whitehead, 427  
*Glanodes* Casey, 440  
*Glycerius* Casey, 439  
*Glyptoderus* Laferté-Sénéctère, 386, 437  
*Glyptoglenus* Bertkau, 384, 435  
*Glyptolenus* Bates, 383–384, 435  
*Goniolophus* Casey, 439  
*Gonoderus* Motschulsky, 435  
*Gynandropus* Dejean, 390, 440  
*Habroscelimorpha* Dokhtouroff, 367  
*Halocoryza* Alluaud, 372, 427  
*Hammatomerus* Chaudoir, 436  
*Haplocoelus* Chaudoir, 435  
*Harpalomerus* Casey, 439  
*Harpalus* Latreille, 389–390, 439  
*Helluomorpha* Laporte, 390  
*Hemicarabus* Gehin, 423  
*Hemiplatynus* Casey, 384, 433  
*Hemisopalus* Casey, 390, 440  
*Heteromorpha* Kirby, 369, 425  
*Hirmoplataphus* Netolitzky, 431  
*Holciophorus* LeConte, 435  
*Hologaeus* Ogueta, 385, 437  
*Homalops* Motschulsky, 447  
*Homoeocarabus* Reitter, 423  
*Hyboptera* Csiki, 399  
*Hydriomicrus* Casey, 431  
*Hydrium* LeConte, 430  
*Hypherpes* Chaudoir, 435  
*Idiochroma* Bedel, 432  
*Isocasonia* Csiki, 444  
*Isoclivina* Kult, 426  
*Isorembus* Jeannel, 388, 438  
*Isotachys* Casey, 381, 430  
*Isotenia* Lapouge, 423  
*Lachnocrepis* LeConte, 438  
*Lachnophorus* Dejean, 394, 443  
*Lagarus* Chaudoir, 436  
*Lamprias* Bonelli, 447  
*Lasioharpalus* Reitter, 439  
*Lebia* Latreille, 395–396, 399, 446



- Lebida* Motschulsky, 447  
*Lebidia* Morawitz, 398  
*Leconteus* Lutschnik, 435  
*Leiotachys* Jeannel, 380, 429  
*Leptoferonia* Casey, 435  
*Leptotachys* Jeannel, 380, 429  
*Leptotrachelus* Latreille, 392, 442  
*Leucagonum* Casey, 433  
*Leuchydrium* Casey, 431  
*Lia* Eschscholtz, 446  
*Lichnocarabus* Reitter, 423  
*Limnastis auctorum*, 381, 430  
*Limodromus* Motschulsky, 433  
*Liocellus* Motschulsky, 439  
*Liocellus* Tschitschérine, 439  
*Liocosmius* Casey, 431  
*Lionepha* Casey, 431  
*Liotachys* Bates, 380  
*Listropus* Putzeys, 370, 427  
*Litoreobracteon* Netolitzky, 431  
*Lopha* Stephens, 431  
*Lophogenius* Motschulsky, 370  
*Lophoglossus* LeConte, 436  
*Loricera* Latreille, 359  
*Loxandrus* LeConte, 383, 385, 436  
*Loxopeza* Chaudoir, 446  
*Lymnastis* Motschulsky, 378–379, 381, 430  
*Lymneops* Casey, 432  
*Lyperopherus* Moschulsky, 436  
*Lyperostenia* Lapouge, 422  
*Macracanthus* Chaudoir, 394–395, 444  
*Macragonum* Casey, 433  
*Masoreus auctorum*, 444  
*Mayaferonia* Ball & Roughley, 436  
*Megacephala* Latreille, 366, 423  
*Megalostylus* Chaudoir, 385, 436  
*Megapangus* Casey, 439  
*Megodontus* Solier, 423  
*Melanagonum* Casey, 433  
*Melanius* Bonelli, 436  
*Melomalus* Casey, 431  
*Melvilleus* Ball, 436  
*Menidius* Chaudoir, 446  
*Meotachys* Erwin, 380  
*Merochlaenius* Grundmann, 437  
*Metabola* Chaudoir, 447  
*Metallina* Motschulsky, 431  
*Metallosomus auctorum*, 433  
*Metamelanius* Tschitschérine, 436  
*Metaxidius* Chaudoir, 390  
*Metriocheila* Thomson, 423  
*Mexiclinidium* Bell & Bell, 428  
*Micragonum* Casey, 433  
*Micratopus* Casey, 378–379, 381, 430  
*Microcallisthenes* Apfelbeck, 423  
*Microcalosoma* Breuning, 422  
*Microlestes* Schmidt-Goebel, 397, 445  
*Micromaseus* Casey, 436  
*Micromelomalus* Casey, 431  
*Microtachys* Casey, 381, 430  
*Microthylax* Rivalier, 367  
*Mimocasonia* Csiki, 444  
*Mioptachys* Bates, 378–380, 429  
*Mischocephalus* Chaudoir, 390  
*Monoferonia* Casey, 435  
*Morio auctorum*, 382, 432  
*Morion* Latreille, 382, 432  
*Mormolyce* Hagenbach, 397  
*Nemotarsus* LeConte, 362, 396  
*Neobrachinus* Erwin, 375, 428  
*Neocalosoma* Breuning, 422  
*Neocarabus* Hatch, 423  
*Neocarabus* Lapouge, 423  
*Neodrypta* Basilewsky, 362  
*Neoreicheia* Kult, 371–373, 427  
*Neotachys* Kult, 381, 430  
*Nestra* Motschulsky, 443  
*Notaphus* Stephens, 431  
*Notiophilus* Duméril, 359  
*Nototylus* Schaum, 358  
*Ochthedromus* LeConte, 430  
*Odacantha* Paykull, 444  
*Odacantha* Perty, 392, 442  
*Odacanthella* Liebke, 444  
*Odacanthina* Csiki, 444  
*Odontium* LeConte, 430  
*Oenaphelox* Ball, 446  
*Omalomorpha* Motschulsky, 447  
*Omaseidius* Jeannel, 435  
*Omaseulus* Lutschnik, 436  
*Omophron* Latreille, 357, 367

- Oodes Bonelli*, 387, 438  
*Oodiellus Chaudoir*, 387, 438  
*Oodinus Motschulsky*, 387, 438  
*Opadius Casey*, 440  
*Ophionea Klug*, 395, 445  
*Ophonus Stephens*, 439  
*Ophryodactylus Chaudoir*, 433  
*Ophryogaster Chaudoir*, 436  
*Opilidia Rivalier*, 367  
*Oreocarabus Gehin*, 423  
*Orsonjohnsonus Hatch*, 435  
*Oxydrepanus Putzeys*, 371–373, 427  
*Oxytselaphus auctorum*, 433  
*Pachychlaenius Grundmann*, 437  
*Pachyteles Perty*, 374, 427  
*Panagaeus (sensu stricto)*, 385  
*Panagaeus Latreille*, 385, 437  
*Parabopha Casey*, 431  
*Parabracteon Notman*, 430  
*Paracalosoma Breuning*, 422  
*Paracarabus Lapouge*, 423  
*Paraclivina Kult*, 372, 426  
*Paracollinus Liebke*, 445  
*Paracolliuris Liebke*, 445  
*Paraferonia Casey*, 436  
*Paragonum Casey*, 433  
*Paralimnastis Jeannel*, 381, 430  
*Parallelomorphus Motschulsky*, 371  
*Paranchomenus Casey*, 432  
*Parapoecilus Jeannel*, 435  
*Paragutor Casey*, 435  
*Paratachys Casey*, 380–381, 430  
*Paratropa Lapouge*, 422  
*Pardileus Gozis*, 439  
*Pelasmus Motschulsky*, 437  
*Pelecium Kirby*, 361  
*Pentacomia Bates*, 424  
*Pentagonica Schmidt-Goebel*, 363, 395, 444  
*Pericompsus (sensu stricto)*, 380  
*Pericompsus LeConte*, 380, 429  
*Perigona (sensu stricto)*, 393  
*Perigona Laporte*, 393, 443  
*Perileptus Schaum*, 377, 429  
*Peristhethus LeConte*, 436  
*Peronoscelis Chaudoir*, 394, 443  
*Peryphodes Casey*, 431  
*Peryphophila Netolitzky*, 431  
*Peryphus Stephens*, 431  
*Petrocharis Ehlers*, 378, 430  
*Phaeoxantha Chaudoir*, 423  
*Pharalus Casey*, 439  
*Pharamecomorphus Motschulsky*, 371  
*Pheropsophidius Hubenthal*, 428  
*Pheropsophus (sensu stricto)*, 375  
*Pheropsophus Solier*, 374, 428  
*Pheryphes Casey*, 436  
*Pheuginus Motschulsky*, 439  
*Philochthemphanes Netolitzky*, 431  
*Philochthus Stephens*, 431  
*Philodes LeConte*, 439  
*Philophuga Motschulsky*, 399, 446  
*Phloeoxena Chaudoir*, 398, 446  
*Piesmus LeConte*, 436  
*Plagiorrhysis Chaudoir*, 445  
*Planetes MacLeay*, 390  
*Plataphodes Ganglbauer*, 431  
*Plataphus Motschulsky*, 431  
*Platyderus Kirby*, 436  
*Platynella Casey*, 384  
*Platynidius Casey*, 433  
*Platynomicrus Casey*, 433  
*Platynus Bonelli*, 383–384, 433  
*Platysma Bonelli*, 435  
*Plectographa Rivalier*, 367  
*Plectralidus Casey*, 439  
*Plesioglymmius Bell and Bell*, 376–377, 428  
*Pleurogenius Motschulsky*, 371  
*Plochionus Latreille & Dejean*, 399, 446  
*Poecilus Bonelli*, 435  
*Pogonidium Ganglbauer*, 431  
*Pogonodaptus Horn*, 388–389, 439  
*Polpochila Solier*, 388  
*Polycheloma Madge*, 446  
*Polyderidius Jeannel*, 381, 430  
*Polyderis Motschulsky*, 380–381, 430  
*Polystichus Bonelli*, 390  
*Pristoscelis Chaudoir*, 436  
*Procolliuris Liebke*, 445  
*Progaleritina Jeannel*, 391–392, 442  
*Protainoa Bell & Bell*, 428

- Protopheropsophus* Hubenthal, 428  
*Pseudanchus* Casey, 432  
*Pseudanomoglossus* Bell, 437  
*Pseudaptinus* Laporte, 390–391, 441  
*Pseudargutor* Casey, 436  
*Pseudocasonia* Liebke, 445  
*Pseudocryobius* Motschulsky, 436  
*Pseudoferonina* Ball, 436  
*Pseudolagarus* Lutschnik, 436  
*Pseudomaseus* Chaudoir, 436  
*Pseudomorpha* Kirby, 357, 368–369, 425  
*Pseudoperiphys* Hatch, 431  
*Pseudophonus* Motschulsky, 439  
*Pseudoplagiorrhysis* Liebke, 445  
*Pterostichus* (*sensu stricto*), 384  
*Pterostichus* Bonelli, 382–384, 435  
*Punctagonum* Grey, 433  
*Refonia* Casey, 435  
*Reichardtula* Whitehead, 372  
*Rembus* Dejean, 438  
*Rhadine* LeConte, 384, 433  
*Rhagocrepis* Eschscholtz, 392, 442  
*Rhombodera* Reiche, 395, 444  
*Scallophorites* Motschulsky, 425  
*Scaphinotus* Latreille, 359  
*Scaris* Chaudoir, 371  
*Scarites* (*sensu stricto*), 370–371  
*Scarites* Fabricius, 370–371, 425  
*Scaritodes* Chaudoir, 370  
*Schizogenius* Putzeys, 370–372, 427  
*Scopodes* Erichson, 395  
*Selenalius* Casey, 390, 440  
*Selenophorus* Dejean, 389–390, 440  
*Semiardistomis* Kult, 373, 427  
*Semicampa* Netolitzky, 431  
*Semiclivina* Kult, 372, 426  
*Sericochlaenius* Grundmann, 437  
*Setalis* Laporte, 384  
*Somotrichus* Seidlitz, 398, 446  
*Spathicus* Nietner, 443  
*Sphaeracra* Say, 392, 442  
*Sphaerotachys* Müller, 380, 429  
*Spongoloba* Chaudoir, 399  
*Stenocellus* Casey, 439  
*Stenocnemus* Mannerheim, 433  
*Stenocrepis* (*sensu stricto*), 387  
*Stenocrepis* Chaudoir, 387, 438  
*Stenolophus* Stephens, 389, 439  
*Stenomophron* Semenov-Tian-Shanskij, 367  
*Stenomorphus* Dejean, 389–390, 441  
*Stenoplatynus* Casey, 384, 433  
*Stenous* Chaudoir, 387, 438  
*Stereagonum* Casey, 433  
*Stereocerus* Kirby, 436  
*Sternocrepis* Chaudoir, 387  
*Steroderus* Motschulsky, 435  
*Steropus* Stephens, 435  
*Stictanchus* Casey, 432  
*Stigmaphorus* Motschulsky, 394, 443  
*Stigmapterus* Motschulsky, 371  
*Stratiotes* Putzeys, 373, 426  
*Stylobracteon* Netolitzky, 431  
*Stylulus* Schaufuss, 378, 430  
*Syncalosoma* Breuning, 422  
*Synechoperyphus* Netolitzky, 432  
*Systolosoma* Solier, 358  
*Tacana* Ball, 446  
*Tachistodes* Casey, 439  
*Tachylopha* Motschulsky, 380, 429  
*Tachymenis* Motschulsky, 380, 429  
*Tachymenis* Wiegmann, 380  
*Tachyphanes* Jeannel, 380, 429  
*Tachys* Stephens, 380–381, 430  
*Tachysalia* Casey, 380, 429  
*Tachysops* Casey, 380, 429  
*Tachyta* Kirby, 378–380, 429  
*Tachyura* Motschulsky, 380, 429  
*Taeniolobus* Chaudoir, 370–371, 425  
*Tainoa* Bell & Bell, 428  
*Tanaocarabus* Reitter, 423  
*Tanystola* Motschulsky, 433  
*Taphranchus* Casey, 432  
*Tapinosthenes* Kolbe, 422  
*Tetracha* Hope, 423  
*Tetragonderus* Dejean, 394  
*Tetragonoderus* Dejean, 443  
*Tetraleucus* Casey, 433  
*Tetraplatypus* Tschitschérine, 439  
*Thalpius* LeConte, 390–391, 441  
*Trachelonepha* Casey, 431  
*Trechicus* LeConte, 443

*Trechonepha* Casey, 431  
*Trepanedoris* Netolitzky, 431  
*Trepanotachys* Alluaud, 380, 429  
*Trichoplataphus* Netolitzky, 431  
*Triliarthrus* Casey, 439  
*Upocompsus* Erwin, 380  
*Xystosomus* Schaum, 378–379  
*Zophium* Gistel, 391, 441  
*Zoyphium* Motschulsky, 391, 441  
*Zuphiosoma* Laporte, 391, 441  
*Zuphium* Latreille, 391, 441

# SPECIES AND SUBSPECIES

*abdominale* Gehin, *Calosoma*, 423  
*abruptus* Darlington, *Paratachys*, 430  
*acuniae* Mutchler, *Cicindela*, 424  
*acuniai* Darlington, *Platynus*, 433  
*acutipennis* Dejean, *Megacephala*, 423  
*addita* Darlington, *Clivina*, 426  
*adonia* Laporte, *Megacephala*, 423  
*adustipennis* Erwin, *Brachinus*, 428  
*aequinoctialis* Chaudoir, *Platynus*, 433  
*aequinoctialis* Linné, *Pheropsophus*,  
 374–375, 428  
*aerata* Putzeys, *Aspidopglossa*, 427  
*aeratus* Reiche, *Selenophorus*, 440  
*affine* Say, *Bembidion*, 432  
*agilis* Laferté-Sénéctère, *Stenocrepis*, 438  
*agonella* Darlington, *Platynus*, 433  
*albipes* Bates, *Pentagonica*, 444  
*albipes* LeConte, *Paratachys*, 430  
*alternans* Chaudoir, *Platynus*, 433  
*alternans* Dejean, *Selenophorus*, 440  
*alticola* Darlington, *Ardistomis*, 427  
*altifluminis* Darlington, *Platynus*, 433  
*amaroides* Dejean, *Oodes*, 438  
*americana* Darlington, *Lymnastis*, 430  
*americana* Linné, *Galerita*, 442  
*americana* Motschulsky, *Pentagonica*, 444  
*americans* Darlington, *Limnastis*, 381  
*americanum* Dejean, *Zuphium*, 441  
*amone* Darlington, *Platynus*, 433  
*aneocupreus* Dejean, *Selenophorus*, 440  
*antiguana* Leng & Mutchler,  
*Megacephala*, 424

*apicale* Jacquelin du Val, *Bembidion*, 432  
*apicalis* Darlington, *Thalpius*, 441  
*apicalis* Fleutiaux & Sallé, *Lebia*, 447  
*aptera* Darlington, *Apenes*, 445  
*arenaria* Darlington, *Halocoryza*, 427  
*argentata* Fabricius, *Cicindela*, 424  
*arimao* Darlington, *Schizogenius*, 427  
*armata* Laporte, *Coptia*, 385  
*armatus* Laporte, *Calosoma*, 423  
*arrogans* Liebke, *Thalpius*, 441  
*asuai* Ogueta, *Panagaeus*, 437  
*atripennis* Putzeys, *Ardistomis*, 427  
*atrorufa* Gundlach, *Pentagonica*, 444  
*autumnalis* Bates, *Mioptachys*, 429  
*bahamensis* Darlington, *Calleida*, 446  
*bahiana* Liebke, *Galerita*, 442  
*baragua* Darlington, *Platynus*, 434  
*basilicus* Chevrolat, *Carabus*, 365, 423  
*beauvoisi* Chaudoir, *Galerita*, 442  
*beauvoisi* Dejean, *Selenophorus*, 440  
*beckwithi* Stephens, *Scarites*, 426  
*bicinctus* Hope, *Somotrichus*, 446  
*bicolor* Leng & Mutchler, *Pentagonica*,  
 444  
*bicolor* Notman, *Polochionus*, 446  
*bierigi* Liebke, *Thalpius*, 441  
*bierigi* Liebke, *Zuphium*, 441  
*biguttata* Putzeys, *Clivina*, 426  
*bipustulata* Fabricius, *Clivina*, 426  
*biramosa* Darlington, *Platynus*, 434  
*biramosa* transcribao Darlington,  
*Platynus*, 434  
*biramosa* uniramosa Darlington, *Platynus*,  
 434  
*bisignata* Leng & Mutchler, *Clivina*, 426  
*blandulus* Schaum, *Pericompsus*, 429  
*boisduvali* Gistel, *Megacephala*, 423  
*boops* Dejean, *Cicindela*, 424  
*boroquense* Bell, *Clinidium*, 428  
*bradycellinus* Hayward, *Tachys*, 430  
*brasiliense* Dejean, *Morion*, 382  
*brevicarinatus* Putzeys, *Oxydrepanus*, 427  
*brevicillus* (Chevrolat), *Macracanthus*,  
 395, 444  
*bromeliarum* Darlington, *Platynus*, 434  
*bruesi* Darlington, *Platynus*, 434

- bruneri Darlington, *Platynus*, 434  
*brunnea* Dejean, *Platynus*, 434  
 brunneus Laporte, *Brachinus*, 428  
 bucheri Darlington, *Platynus*, 434  
 calathina Darlington, *Platynus*, 434  
*capito* Bates, *Polyderis*, 430  
 carabiai Darlington, *Platynus*, 434  
 cardini Leng & Mutchler, *Cicindela*, 424  
 carib Darlington, *Paratachys*, 430  
 caribbeana Darlington, *Pseudomorpha*, 425  
 cariniger Putzeys, *Selenophorus*, 440  
 carolina Linné, *Megacephala*, 423  
*carolinensis* Latreille, *Megacephala*, 424  
 caymanensis Darlington, *Calleida*, 446  
 celeris Dejean, *Loxandrus*, 436  
 centralis Darlington, *Dyschromus*, 435  
 chalcites Say, *Pterostichus*, 436  
 chalybaea Dejean, *Platynus*, 434  
 chalybaeus Dejean, *Glyptolenus*, 435  
 chalybaeus Dejean, *Selenophorus*, 440  
 chaudiiri Ball, *Stenognathus*, 398  
*chevrolati* Gemminger & Harold, *Bembidion*, 432  
 chiolinoi Bell, *Clinidium*, 428  
*chlorocephala* Mannerheim, *Cicindela*, 425  
*chokoloskei* Leng, *Selenophorus*, 440  
 christophe Darlington, *Platynus*, 434  
 ciliatus Mutchler, *Aepheidius*, 395, 444  
 cinchonae Darlington, *Platynus*, 434  
 cinctus Putzeys, *Selenophorus*, 440  
*circumcinctus* Say, *Chlaenius*, 438  
*clientulum* Casey, *Agonum*, 433  
 coamensis Mutchler, *Dyschirius*, 426  
 collaris Dejean, *Galerita*, 392  
*collusor* Casey, *Cicindela*, 424  
 columbus Darlington, *Perileptus*, 429  
*comma* Putzeys, *Aspidoglossa*, 427  
 compactus Bell & Bell, *Plesioglymmius*, 428  
*complanatus* Fabricius, *Pheropsophus*, 428  
 concolor Ball, *Ochropisus*, 398  
 constricticeps Darlington, *Platynus*, 434  
*convexicollis* LeConte, *Stenolophus*, 439  
 convexulus Darlington, *Acupalpus*, 439  
 coptoderoides Darlington, *Agonum*, 433  
 cordatum Chaudoir, *Morion*, 382  
 coriacea Chevrolat, *Apenes*, 445  
 corumbana Liebke, *Galerita*, 392  
 costata Darlington, *Phloeoxena*, 446  
 costigerus Darlington, *Morion*, 432  
 crenatus LeConte, *Loxandrus*, 437  
*cruentatus* Chevrolat, *Loxandrus*, 437  
 cubae Darlington, *Clivina*, 426  
 cubana Leng & Mutchler, *Cicindela*, 424  
 cubanum Darlington, *Bembidion*, 432  
 cubanum Liebke, *Zuphium*, 442  
 cubanus Bänninger, *Scarites*, 426  
 cubanus Chaudoir, *Chlaenius*, 438  
 cubanus Chaudoir, *Pseudaptinus*, 441  
 cubanus Darlington, *Bradycellus*, 439  
 cubanus Darlington, *Stenomorphus*, 390, 441  
 cubanus Tschitschérine, *Loxandrus*, 437  
 cubax Darlington, *Paratachys*, 430  
 cubensis Darlington, *Platynus*, 434  
 cubensis Darlington, *Pterostichus*, 436  
 cuprascens Motschulsky, *Platynus*, 434  
*cuprascens* Roeschke, *Calosoma*, 423  
*cupreomicans* Sturm, *Pterostichus*, 436  
*cuprinus* Dejean, *Selenophorus*, 440  
 cupripennis Chaudoir, *Dyschromus*, 435  
 curvicosta Chevrolat, *Clinidium*, 428  
*cyaneo-nigra* Chaudoir, *Megacephala*, 423  
 cyaneolimbatus Chevrolat, *Ardistomis*, 427  
 cyaneopacus Darlington, *Selenophorus*, 440  
*cyanescens* Motschulsky, *Agonum*, 433  
 cychrina Darlington, *Platynus*, 434  
 danforthi Darlington, *Scarites*, 426  
 darlingtoni Bänninger, *Scarites*, 426  
 darlingtoni Bell, *Clinidium*, 428  
 darlingtoni Mutchler, *Bembidion*, 432  
 dealata Darlington, *Phloeoxena*, 446  
 deceptor Darlington, *Pseudaptinus*, 441  
*decepiens* Dejean, *Bembidion*, 432  
 decolor Chaudoir, *Calleida*, 446  
 dejeani Chaudoir, *Platynus*, 434  
 delauneyi Fleutiaux & Sallé, *Pachyteles*,

427

*delicata* Darlington, *Apenes*, 445  
*denticollis* Chaudoir, *Scarites*, 426  
*dentifer* Darlington, *Perileptus*, 429  
*dentiger* LeConte, *Dyschirius*, 426  
*dentipes* Dejean, *Clivina*, 426  
*dimidiata* Chaudoir, *Galerudicia*, 446  
*discopunctatus* Dejean, *Selenophorus*, 440  
*divisa* Darlington, *Pentagonica*, 444  
*dominicanus* Darlington, *Paratachys*, 430  
*dominicensis* Chaudoir, *Omophron*, 367  
*dorsalis* Brullé, *Thalpius*, 441  
*dorsalis castissima* Bates, *Cicindela*, 424  
*dorsalis Fabricius*, *Leptotrachelus*, 442  
*dorsalis Say*, *Cicindela*, 424  
*dorsalis venusta* Laferté-Sénéctère,  
*Cicindela*, 424  
*dubius* Putzeys, *Selenophorus*, 440  
*duodecimstriata* Chevrolat, *Stenocrepis*,  
438  
*effeminata* Darlington, *Coptia*, 437  
*egaensis* Thomson, *Cicindela*, 424  
*eggersi* Ehlers, *Stylulus*, 430  
*elegans* Chaudoir, *Calleida*, 446  
*elegantulus* Laferté-Sénéctère,  
*Pericompsus*, 429  
*elevatus* Fabricius, *Somotrichus*, 446  
*elliptica* Chaudoir, *Platynus*, 434  
*elongata* Chaudoir, *Platynus*, 434  
*elongatulum auctorum*, *Agonum*, 433  
*elongatulus* Putzeys, *Ardistomis*, 427  
*ensenadae* Mutchler, *Tachys*, 430  
*erthrodera* Brullé, *Galerita*, 442  
*erythrocerus* LeConte, *Dyschirius*, 426  
*estriata* Darlington, *Platynus*, 434  
*exaratus* Laferté-Sénéctère, *Chlaenius*,  
437  
*excisus* Putzeys, *Selenophorus*, 441  
*expansa* Casey, *Diplocheila*, 438  
*extensicolle cubanum* Darlington,  
*Agonum*, 433  
*extensicolle Say*, *Agonum*, 433  
*faber* Darlington, *Platynus*, 434  
*fallax* Dejean, *Bembidion*, 432  
*fasciatus* Say, *Panagaeus*, 437  
*fastidiosus* Laferté-Sénéctère, *Bembidion*,

432

*femoralis* Chaudoir, *Stenocrepis*, 438  
*festinans* Casey, *Bradycellus*, 439  
*festiva* Dejean, *Coptodera*, 446  
*filax* Darlington, *Paratachys*, 430  
*flavilabris cubanus* Darlington,  
*Selenophorus*, 440  
*flavilabris* Dejean, *Selenophorus*, 440  
*flavipes* LeConte, *Pentagonica*, 444  
*flavipes picipes* Darlington, *Pentagonica*,  
444  
*floridanus* Horn, *Chlaenius*, 438  
*floridanus* LeConte, *Loxandrus*, 437  
*forreri* Bates, *Carabus*, 365  
*fosser* Degeer, *Scarites*, 426  
*fractilinea* Darlington, *Platynus*, 434  
*fratrorum* Darlington, *Platynus*, 434  
*frenata* Chaudoir, *Lebia*, 447  
*frenata chevrolati* Blackwelder, *Lebia*, 447  
*gaudens* Casey, *Agonum*, 433  
*geniculata* Bates, *Phloeoxena*, 398  
*georgiae* Palisot, *Morion*, 382  
*gibba* Darlington, *Lebia*, 447  
*gigas* Bonelli, *Enceladus*, 368, 425  
*gilvipes* Chaudoir, *Stenocrepis*, 438  
*gilvipes* Mannerheim, *Brachinus*, 428  
*glabrella* Motschulsky, *Perigona*, 443  
*gracilis* Casey, *Stenolophus*, 439  
*grimmi* Sturm, *Harpalus*, 440  
*grossus* Say, *Euryderus*, 390  
*guadeloupensis* Fleutiaux & Sallé,  
*Amblygnathus*, 441  
*guadeloupensis* Fleutiaux & Sallé,  
*Cicindela*, 425  
*guadeloupensis* Fleutiaux & Sallé,  
*Perigona*, 443  
*guadeloupensis* Fleutiaux & Sallé,  
*Selenophorus*, 440  
*guadeloupensis* Gory, *Apenes*, 445  
*guadeloupensis* Kult, *Ardistomis*, 427  
*guadeloupensis* Putzeys, *Aspidoglossa*,  
427  
*guerin* Gory, *Cicindela*, 424  
*guildingi* Kirby, *Clinidium*, 428  
*gundlachi* Chaudoir, *Chlaenius*, 438  
*gundlachi* Darlington, *Colliuris*, 445

- gundlachi* Leng & Mutchler, *Ardistomis*, 427
- gyllenhali* Dejean, *Pachyteles*, 427
- haitianum* Darlington, *Zuphium*, 442
- haitianus* Darlington, *Eucaerus*, 443
- haitianus* Darlington, *Selenophorus*, 440
- haitiense* Bell, *Clinidium*, 428
- hamiferum* Chaudoir, *Bembidion*, 432
- harpaloides* Reiche, *Selenophorus*, 440
- hebraea* Putzeys, *Cicindela*, 425
- hendrichsi* Bolivar, *Carabus*, 365
- hieroglyphica* Klug, *Cicindela*, 425
- hispaniolae* Darlington, *Tachyta*, 380, 429
- humboldti* Gistel, *Galerita*, 442
- humidens* Chevrolat, *Clinidium*, 428
- imitatrix* Darlington, *Phloeoxena*, 446
- immaculatus* Bates, *Pericompsus*, 429
- incis* Bell, *Clinidium*, 428
- infimus* Bates, *Loxandrus*, 436
- infuscatus* Dejean, *Stenolophus*, 439
- insulana* Jacquelin du Val, *Stenocrepis*, 438
- insularis* Darlington, *Eucaerus*, 443
- insularis* Darlington, *Micratopus*, 430
- insularis* Darlington, *Mioptachys*, 429
- insularis* Jacquelin du Val, *Clivina*, 426
- insularis* Laporte, *Galerita*, 442
- insularis* Mutchler, *Pseudaptinus*, 441
- integer* Fabricius, *Harpalus*, 440
- interruptus* Herbst, *Scarites*, 426
- intersectus* (Germar), *Tetragonoderus*, 443
- iracunda* Putzeys, *Stratiotes*, 426
- iridens* Motschulsky, *Acupalpus*, 439
- iridescens* Chaudoir, *Athrostictus*, 441
- jaegeri* Dejean, *Platynus*, 434
- jaegeri* Mannerheim, *Platynus*, 434
- jamaicae* Darlington, *Chlaenius*, 438
- jamaicense* Arrow, *Clinidium*, 428
- jamaicense* Darlington, *Bembidion*, 432
- jamcubanus* Erwin, *Pericompsus*, 429
- jeanneli* Darlington, *Perileptus*, 429
- l'herminieri* Chaudoir, *Platynus*, 434
- lacordairei* Degean, *Pseudomorpha*, 368
- laetificum* Darlington, *Agonum*, 433
- laeviceps* Darlington, *Platynus*, 434
- laevicincta* Darlington, *Apenes*, 445
- laevicollis* Reiche, *Euphorticus*, 443
- laevigata* Bates, *Perigona*, 443
- laevissima* Chaudoir, *Pseudomorpha*, 368
- laevistriatus* Fleutiaux & Sallé, *Ardistomis*, 427
- laportei* Chevrolat, *Megacephala*, 423
- lata* Darlington, *Apenes*, 445
- latelytra* Darlington, *Platynus*, 434
- laticus* Darlington, *Selenophorus*, 440
- lebioides* Bates, *Glyptolenus*, 435
- lecontei* Dejean, *Galerita*, 442
- lecontei* tenebricosa Klug, *Galerita*, 442
- leucopterus* Chevrolat, *Anchonoderus*, 443
- leucopterus* Chevrolat, *Lachnophorus*, 443
- limbata* Waterhouse, *Colliuris*, 445
- limbipennis* Jacquelin du Val, *Clivina*, 426
- lineatopunctatus* Dejean, *Selenophorus*, 440
- longilabris* Say, *Cicindela*, 424
- lucidulus* Dejean, *Selenophorus*, 440
- lucorum* Gistel, *Cicindela*, 424
- ludovicianus* Leng, *Chlaenius*, 437
- lugens* Chaudoir, *Galerita*, 442
- macer* Darlington, *Platynus*, 434
- macleayi* Kirby, *Selenophorus*, 440
- macrodentra* Chevrolat?, *Pericompsus*, 430
- maculicornis* Laporte, *Megacephala*, 424
- major* LeConte, *Diplocheila*, 388, 438
- major* melissisa Ball, *Diplocheila*, 439
- mannerheimi* Chaudoir, *Platynus*, 434
- mannerheimi* Putzeys, *Ardistomis*, 427
- manni* Darlington, *Stenomorphus*, 390, 441
- marca* Darlington, *Platynus*, 434
- marginalis* Dejean, *Apenes*, 445
- marginata* Fabricius, *Cicindela*, 424
- marginicollis* Darlington, *Thalpius*, 441
- marginicollis* fumipes Darlington, *Thalpius*, 441
- marginipennis* Putzeys, *Clivina*, 427
- massiliensis* Fairmaire, *Somotrichus*, 446
- maxillosus* Horn, *Chlaenius*, 437
- media* Darlington, *Platynus*, 434
- medioptera* Darlington, *Platynus*, 434

- megacephalus Hlavac, Scarites, 426  
*melanaria* Erichson, *Galerita*, 442  
 memnonia Dejean, Platynus, 434  
 menevillei Chaudoir, Chlaenius, 386  
 metallica Dejean, Stenocrepis, 438  
*mexicana* Gray, *Megacephala*, 424  
 mexicanum Chaudoir, Zuphium, 442  
*mexicanus* Chaudoir, *Anatrichis*, 438  
*micans* Chaudoir, *Pterostichus*, 436  
 microcostata Darlington, *Galerita*, 442  
 microps Darlington, *Perigona*, 443  
 minutus Darlington, *Perileptus*, 429  
*misella* Chaudoir, *Cicindela*, 424  
*montana* Darlington, *Galerita*, 442  
 montana Darlington, *Phloeoxena*, 446  
*montana* Mutchler, *Scarites*, 426  
 morantensis Erwin, *Pericompsus*, 430  
 mundus Putzeys, *Selenophorus*, 440  
*mutans* Darlington, *Loxandrus*, 436  
 mutchleri Bänninger, *Scarites*, 426  
 nana inornata, *Tachyta*, 380  
*nasutus* Schaufuss, *Stylulus*, 430  
*niger* Gory, *Euphorticus*, 443  
 niger Randall, *Chlaenius*, 437  
 nigriceps Dejean, *Perigona*, 443  
 nigricornis Darlington, *Pentagonica*, 444  
 nigrita Darlington, *Lebia*, 447  
 nigroclarus Darlington, *Ardistomis*, 427  
 nitidipennis Darlington, *Ardistomis*, 427  
 noah Darlington, *Colliuris*, 445  
 nocticolor Darlington, *Loxandrus*, 437  
 noctis Darlington, *Mioptachys*, 429  
 nonseriatus Darlington, *Selenophorus*, 440  
 nubicola Darlington, *Lebia*, 447  
*obliquus* Brullé, *Pheropsophus*, 428  
*oblonga* Casey, *Diplocheila*, 438  
*obscura* Laporte, *Coptodera*, 446  
*obscurata* Chaudoir, *Megacephala*, 424  
*obscuratum* Chaudoir, *Agonum*, 433  
 occidentalis (Olivier), *Galerita*, 392  
 occidentalis Klug, *Megacephala*, 424  
 ochropezus Say, *Stenolophus*, 439  
 olivacea Chaudoir, *Cicindela*, 424  
 opaca LeConte, *Apenes*, 445  
 opacus Chaudoir, *Dyschromus*, 435  
 orientale Dejean, *Morion*, 382  
 ovalis Darlington, *Apenes*, 445  
 pallens Fabricius, *Polochionus*, 446  
*pallida* Chevrolat, *Pachyteles*, 427  
 pallidus Erwin, *Brachinus*, 375  
*pallipennis* LeConte, *Perigona*, 443  
*pallipes* Brullé, *Stenocrepis*, 438  
 pallipes Fabricius, *Apenes*, 445  
*pallipes* Fleutiaux & Sallé, *Cicindela*, 424  
*pallipes* LeConte, *Pentagonica*, 444  
*pallipes* Reiche, *Stenocrepis*, 438  
 palustris Darlington, *Stenocrepis*, 438  
 panamensis Laferté-Sénéctère, *Panagaeus*, 385  
 parallela Dejean, *Apenes*, 445  
 parallela inaguae Darlington, *Apenes*, 445  
*particeps* Casey, *Bembidion*, 432  
 parumpunctatus Dejean, *Selenophorus*, 440  
 parviceps Darlington, *Micratopus*, 430  
 parvus Darlington, *Selenophorus*, 440  
 paulax Darlington, *Paratachys*, 430  
 pavens Darlington, *Platynus*, 434  
 perezi Darlington, *Dyschromus*, 435  
 perplexus Dejean, *Chlaenius*, 437  
 philipi Erwin, *Pericompsus*, 430  
 picea Darlington, *Perigona*, 443  
*picea* Fleutiaux & Sallé, *Pentagonica*, 444  
 piceolus Laferté-Sénéctère, *Paratachys*, 430  
 piceus Motschulsky, *Anatrichis*, 438  
 picta Chaudoir, *Colliuris*, 445  
 picta concluda Liebke, *Colliuris*, 445  
 picta extrema Liebke, *Colliuris*, 445  
 pinarensis Darlington, *Platynus*, 434  
 plagiata Darlington, *Phloeoxena*, 446  
 planum Chevrolat, *Clinidium*, 428  
*planus* Olivier, *Pheropsophus*, 428  
 platycephalus Reichardt, *Pheropsophus*, 375  
*poeyi* Chevrolat, *Chlaenius*, 438  
 poeyi Jacquelin du Val, *Microlestes*, 446  
*porcata* Klug, *Galerita*, 442  
 portoricense Darlington, *Bembidion*, 432  
 portoricensis Darlington, *Apenes*, 445  
 portoricensis Darlington, *Phloeoxena*, 446  
 portoricensis Liebke, *Colliuris*, 445



- pretiosa* Chaudoir, *Calleida*, 446  
*procera* Casey, *Diplocheila*, 438  
*propinquus* Putzeys, *Selenophorus*, 440  
*proximum* Harris, *Agonum*, 433  
*puberulus* Putzeys, *Selenophorus*, 440  
*pubescens aeneolus* Bates, *Euphorticus*, 443  
*pubescens* Dejean, *Euphorticus*, 443  
*pubifer* Putzeys, *Selenophorus*, 440  
*puertoricensis* Mutchler, *Selenophorus*, 440  
*puncticeps compacta* Darlington, *Platynus*, 434  
*puncticeps* Darlington, *Platynus*, 434  
*puncticollis* Putzeys, *Amblygnathus*, 441  
*puncticollis* Putzeys, *Selenophorus*, 440  
*punctifrons* Chaudoir, *Caelostomus*, 436  
*punctus* Darlington, *Platynus*, 434  
*puntifrons* Chaudoir, *Caelostomus*, 384  
*purpurata* Fleutiaux & Sallé, *Apenes*, 445  
*putzeysi* Fleutiaux & Sallé, *Paratachys*, 430  
*pygmaeus* Dejean, *Thalpius*, 441  
*pyritosus* Dejean, *Selenophorus*, 440  
*quadrimalculata* Palisot de Beauvois, *Clivina*, 426  
*quadrisingatus* Chevrolat, *Panagaeus*, 437  
*ramoni* Darlington, *Platynus*, 434  
*ramosi* Darlington, *Selenophorus*, 441  
*ramsdeni* Darlington, *Ardistomis*, 427  
*rectangulus* LeConte, *Loxandrus*, 436  
*reichei* Putzeys, *Pericompsus*, 429  
*reicheoides* Darlington, *Oxydrepanus*, 427  
*ridiculus* Schaufuss, *Polyderis*, 430  
*rivieri* Reichardt, *Pheropsophus*, 374  
*rostratus* Darlington, *Pogonodaptus*, 439  
*roysi* Darlington, *Platynus*, 434  
*rubiventris* LeConte, *Dyschirius*, 426  
*rubricollis* Dejean, *Calleida*, 446  
*rucillum* Darlington, *Bembidion*, 432  
*ruficollis* Dejean, *Galerita*, 442  
*rufipes* Dejean, *Colliuris*, 445  
*rufipes insignis* Chaudoir, *Colliuris*, 445  
*rufiventris* Dejean, *Cicindela*, 424  
*rufoclarus* Darlington, *Ardistomis*, 427  
*rufus* Putzeys, *Oxydrepanus*, 427  
*rutilans confusa* Chaudoir, *Megacephala*, 424  
*rutilans infusca* Mannerheim, *Megacephala*, 424  
*rutilans* Thomson, *Megacephala*, 424  
*rutilus* Chevrolat, *Diplochaetus*, 429  
*salebrosus* Liebke, *Pseudaptinus*, 441  
*sauleyi* Schaupp, *Cicindela*, 424  
*sauricollis* Darlington, *Coptia*, 437  
*sayi* Brullé, *Pterostichus*, 436  
*sayi* Dejean, *Calosoma*, 423  
*schaefferi* Horn, *Cicindela*, 424  
*schwarzi* Darlington, *Phloeoxena*, 446  
*scripta* Darlington, *Platynus*, 434  
*scriptella* Darlington, *Platynus*, 434  
*selleanus* Darlington, *Bradycellus*, 439  
*sellensis* Darlington, *Platynus*, 434  
*semicrenata* Chaudoir, *Aspidoglossa*, 427  
*sericeus* Darlington, *Apristus*, 445  
*serpens* LeConte, *Cicindela*, 425  
*sigmoidea* Chaudoir, *Cicindela*, 425  
*sigmoidea* LeConte, *Cicindela*, 425  
*simplex* Chevrolat, *Clivina*, 426  
*simplex* LeConte, *Agonum*, 433  
*simplicicollis* Darlington, *Glyptolenus*, 435  
*sinuatus* Gyllenhal, *Selenophorus*, 441  
*solitarius* Darlington, *Selenophorus*, 441  
*sparsum* Bates, *Bembidion*, 432  
*spinipes* Sulzer, *Scarites*, 426  
*splendida* Dokhtouroff, *Megacephala*, 424  
*splendidum* Dejean, *Calosoma*, 423  
*spretum* Dejean, *Bembidion*, 432  
*strandi* Liebke, *Apenes*, 445  
*striata* Klug, *Galerita*, 442  
*striatopunctatus* Putzeys, *Selenophorus*, 441  
*striax* Darlington, *Paratachys*, 430  
*subaeneus* Reiche, *Selenophorus*, 441  
*subangusta* Darlington, *Platynus*, 435  
*subcordens* Darlington, *Platynus*, 435  
*subdepressa* Darlington, *Stenocrepis*, 438  
*sublaevis* Putzeys, *Dyschirius*, 426  
*subovalis* Darlington, *Platynus*, 435  
*subquadratus* Putzeys, *Selenophorus*, 441  
*subterraneus alternans* Chaudoir, *Scarites*, 426

- subterraneus* Bonelli, *Scarites*, 426  
*subterraneus* Fabricius, *Scarites*, 426  
*subterraneus* patruelis LeConte, *Scarites*, 426  
*subtilis* Bates, *Anchonoderus*, 443  
*sulcata* Chevrolat, *Stenocrepis*, 438  
*sulcatus* (Fabricius), *Rhysodes*, 376  
*sulcicollis* Jacquelin du Val, *Apenes*, 445  
*suturalis* Chaudoir, *Colliuris*, 445  
*suturalis* Fabricius, *Cicindela*, 424  
*suturalis* hebraea Klug, *Cicindela*, 425  
*suturalis* nocturna Steinheil, *Cicindela*, 425  
*taitenis* Boheman, *Cicindela*, 424  
*tericola* Darlington, *Lebia*, 447  
*testaceolimbata* Motschulsky, *Perigona*, 443  
*tetrastigma* caymanensis Darlington, *Colliuris*, 445  
*tetrastigma* Chaudoir, *Colliuris*, 445  
*thaxteri* Darlington, *Pseudaptinus*, 441  
*thespis* Casey, *Bembidion*, 432  
*thoracica* Chevrolat, *Galerita*, 442  
*thoracicus* Putzeys, *Selenophorus*, 441  
*tibialis* Chevrolat, *Stenocrepis*, 438  
*tiburoncus* Darlington, *Dyschromus*, 435  
*tinctula* Darlington, *Calleida*, 446  
*tipoto* Darlington, *Platynus*, 435  
*tortuosa* Dejean, *Cicindela*, 425  
*tortuosa* LeConte, *Cicindela*, 425  
*translucens* Darlington, *Tachys*, 430  
*trifasciata ascendens* LeConte, *Cicindela*, 425  
*trifasciata* Dejean, *Cicindela*, 425  
*trifasciata* Fabricius, *Cicindela*, 425  
*trifasciata* LeConte, *Cicindela*, 425  
*tristis* Reiche, *Galerita*, 442  
*tritax* Darlington, *Elaphropus*, 429  
*trivittatus* LeConte, *Euproctinus*, 446  
*tropicalis* Motschulsky, *Cicindela*, 425  
*turquinensis* Darlington, *Platynus*, 435  
*turquinum* Darlington, *Bembidion*, 432  
*umbripennis* LeConte, *Perigona*, 443  
*unicolor* Chevrolat, *Coptodera*, 446  
*unicolor* Latreille & Dejean, *Galerita*, 442  
*unifasciatus* Dejean, *Somotrichus*, 446  
*vagepunctata* Darlington, *Platynus*, 435  
*variegata* Dejean, *Apenes*, 445  
*variegata* Dejean, *Cicindela*, 424  
*velatus* Darlington, *Bradycellus*, 439  
*vetula* Chevrolat, *Galerita*, 442  
*vigilans* Casey, *Agonum*, 433  
*virens* Chaudoir, *Chlaenius*, 438  
*virginica* Olivier, *Megacephala*, 423  
*virginicum* Casey, *Calosoma*, 423  
*virgula* Thomson, *Megacephala*, 424  
*viride* LeConte, *Agonum*, 433  
*viridicolle* Laferté-Sénéctère, *Bembidion*, 432  
*viridicollis* Dejean, *Cicindela*, 425  
*viridiflavescens* Horn, *Cicindela*, 425  
*viridiflavescens originalis* Horn, *Cicindela*, 425  
*visitor* Darlington, *Platynus*, 435  
*vitraci* Fleutiaux & Sallé, *Amblygnathus*, 441  
*vittiger* LeConte, *Tachys*, 430  
*vittula* Darlington, *Pentagonica*, 444  
*vulnerata* Putzeys, *Aspidoglossa*, 427  
*wolla* Darlington, *Platynus*, 435  
*xenopodium* Bell, *Clinidium*, 428  
*yunax* Darlington, *Elaphropus*, 429

## BOOK REVIEW

Kryzhanovsky, O.L. 1983. - Fauna of the U.S.S.R., new series no. 128, Coleoptera. Volume I, no. 2. Adephaga (Part 1), 341 pp., Leningrad (Zoological Institute of the Academy of Sciences).

The fauna of the U.S.S.R. occupies a particularly vast geographic region encompassing a major portion of the Palearctic domain, from the Baltic Sea and Carpathian Mountains to Kamchatka and the northern-most part of Pamir.

This region includes zones as diverse as taigas and boreal forests, plains, steppes and deserts of Russia and Central Asia, high mountains such as the Caucasus, the Urals and the northern foothills of the Himalaya, and even a part of the Far East, thus comprising extremely abundant and varied ecosystems and habitats. Over several decades, nearly 200 volumes have been published as part of this monumental series, and the subject is far from being exhausted, since many groups of animals have not yet been covered.

Dr. O.L. Kryzhanovsky, of the Zoological Institute of the Academy of Sciences in Leningrad, has just published the first of a series of volumes on Adephaga, a suborder of Coleoptera mainly constituted by the family Carabidae. This is a long awaited work and one must be delighted to see its first part being written by such a competent author, who is one of the foremost experts on this family, having at his disposal enormous collections from these regions.

Following a general coverage of the suborder and its origin, based particularly on the masterly works of A.G. Ponomarenko on Mesozoic Coleoptera, and of their subdivisions, the author proceeds to the superfamily Caraboidea, which he divides into three families. The first two (Rhysodidae and Trachypachidae), with few species, are treated very thoroughly in 30 pages. This is a very instructive discussion because, up to now, the positions and affinities of these groups have been the object of controversy, and what Kryzhanovsky says will probably help to bring this to an end.

The author then proceeds to the family Carabidae and presents, in more than 160 pages, an extremely thorough and careful overview of its members on a worldwide basis. Every aspect is treated with style and depth, particularly morphology, terminology, biology and geographic distribution; the last in 70 pages is especially interesting, not only because it presents updated data on the distribution of these Coleoptera in the world, but also because it includes an in-depth study of the various faunal regions of the U.S.S.R. The systematic classification adopted is that proposed by Kryzhanovsky in 1976, which represented a notable advance on what was available up to then, but which will still require additional modification.

A review of the Carabidae of this vast country is then undertaken. Because the fauna comprises more than 2200 species in this region, with many yet to be described, about 20 volumes will be needed to complete this exhaustive revision. This will be a considerable task, already quite advanced by Kryzhanovsky and a few collaborators whom he trained to that aim. Many years will be necessary to carry out such work. Consequently, to allow the numerous carabidologists of that country to classify their collections, the author provides, in 75 pages, a brief but comprehensive and abundantly illustrated overview of the Carabidae of the U.S.S.R., with clear and precise keys to all genera and subgenera represented in the fauna.

Finally one finds a comprehensive bibliography indicating the degree to which the author is aware of all that has been published on the subject.

This first volume, which the experienced carabidologist will find indispensable, gives an idea of the importance of the following volumes which will be impatiently awaited.

The work is written in Russian, which may cause difficulties to most western coleopterists. But I believe it will soon be translated into English and published in America, as has already happened to some others of the author's works and to many other volumes of the Fauna of the U.S.S.R.

P.Basilewsky<sup>1</sup>  
Musée Royal de l'Afrique Centrale  
B-1980  
Tervuren  
Belgium

---

<sup>1</sup>Translated from French by J. F. Landry, Department of Entomology, University of Alberta, Edmonton, Canada.

## EDITOR'S ACKNOWLEDGEMENTS

Dr. George E. Ball, long time editor of *Quaestiones Entomologicae*, began a well-earned administrative leave of absence this summer after serving with distinction for 10 years as Chairman of the Department of Entomology, University of Alberta and for one year each as First and Second Vice-President, President and Past-President of the Entomological Society of Canada. Before leaving for Europe in June with his wife Kaye, George asked me to serve as Acting Editor of the journal for one year. Thus, it falls to me the pleasant task of thanking those individuals, listed below, who served as reviewers of the papers appearing in Volume 20:

W.G. Evans, Department of Entomology, University of Alberta, Edmonton, AB  
L.H. Herman, Department of Entomology, American Museum of Natural History, New York, NY  
G.J. Hilchie, Department of Entomology, University of Alberta, Edmonton, AB  
H.F. Howden, Department of Biology, Carleton University, Ottawa, Ont.  
J. Klimaszewski, Lyman Entomological Museum, Macdonald College, McGill University, Ste. Anne du Bellevue, Que.  
R.E. Leech, Department of Entomology, University of Alberta, Edmonton, AB  
I.C. McDonald, Metabolism and Radiation Research Laboratory, USDA, Fargo, ND  
A.F. Newton, Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, MA  
G.R. Noonan, Section of Invertebrate Zoology, Milwaukee Public Museum, Milwaukee, WI  
E.M. Pike, Fairview, AB  
D.I. Southern, Department of Zoology, University of Manchester, Manchester, U.K.  
J.R. Spence, Department of Entomology, University of Alberta, Edmonton, AB

I would also like to acknowledge the cheerful assistance in this department of D. Shpeley and J. Scott in reading proof and of J.-F. Landry in translating abstracts of some of the papers into French.

Publication of this issue of Volume 20 also marks the end of year five of Mrs. S. Subbarao's sojourn as Publications Manager of the journal and I wish to thank her for her continuing high level of interest and performance in executing the many, often tedious, tasks required of this position. It is also due to her efforts that publication of the journal is, at long last, back on schedule.

Finally, I would like to thank those authors who selected *Quaestiones Entomologicae* for publication of their work and the small, and we would like to think select, body of faithful subscribers and readers whose continued support of the journal makes our effort in producing it worthwhile.

Before signing off I wish to comment on a few of the manuscripts recently submitted for publication. While all manuscripts we published this year were acceptable in content and organization, I noticed a lack of attention to detail in the final preparation of some of them that may relate to George Ball's well known generosity as an editor— details like uncited papers appearing in the list of references and vice versa; incomplete literature citations; inconsistent use of numerals and words for numbers; inconsistent spelling of scientific names etc.— all items fully covered in most manuals on scientific writing. When George receives such a manuscript and its content is basically sound, he has it reviewed, accepts it, makes all the (often considerable) changes required himself and passes it on to Mrs. Subbarao, for processing. He

does this because he wants the paper for *Quaestiones Entomologicae*, and because he accepts only the highest quality of presentation. Because of his countless other responsibilities he also sometimes spreads himself too thin and misses some details or adds some inconsistencies of his own to the manuscripts. When these errors appear in print, they upset the author and are usually laid at Mrs. Subbarao's door. Too many authors seem to be willing to have George do the final cleaning up of their manuscripts.

Another continuing problem is that of authors adding items or removing them from the galleys of their manuscripts. These changes are time-consuming and expensive for Mrs. Subbarao to implement and often result in new errors not there before creeping into the manuscript. Also, authors often make such changes in only one place in the manuscript when the same change might be required elsewhere. When this happens, the deletion or addition adds a new inconsistency to the manuscript that the author and/or editor may not catch until he sees the final product. For this reason we prefer that such changes not be made at this stage of production.

Consistency and attention to detail are the responsibility of author, editor and production manager; but, after publication, it is the author who "reaps the whirlwind". Thus I would ask that future contributors please attend fully to these little details before submitting and save George some work when he returns. This effort will, I'm sure, also result in more satisfied authors.

B.S. Heming  
Acting Editor

## INDEX TO VOLUME 20

- , *et al.*, 32  
 Ab'Sáber, A.N., 76  
*Acalypha*, 72  
*acomus* Ratcliffe, n. sp., *Brasilucanus*, 63, 65, 67  
*Affinoptochus*, 9  
 Agatsuma, T., 54  
*Alangium*, 72  
*Aleochara*, 9–10  
 Aleocharinae, 8–10, 13–15  
 Aleocharini, 12–13, 15  
*algidus* LeConte, *Pterostichus*, 4  
*Alianta*, 14  
 Allen, A.J., 38  
*alvarengai* Vulcano and Pereira, *Brasilucanus*, 62–63, 65, 83  
*Ammophila azteca*, 32  
 Amos, A., 91–92, 94, 100, 102  
*anicia* Doubleday, *Melitaea*, 35, 41–42  
*Anomognathus*, 9  
*Anthocharis creusa* Doubleday, 35, 41–42  
*Apterochylus* Waterhouse, 77  
 Araujo, J., 12  
*Argynnis astarte* Doubleday, 35, 41  
*Argynnis victoria*, 37  
 Arnett, R.H., 8  
 Arrow, G., 62, 65  
 Ashe, J.S., 10  
 Asperen, K. van,  
     *see* Velthuis, H.H.W., 54  
*astarte* Doubleday, *Argynnis*, 35, 41  
*Astenus*, 11  
*Astenus procerus* (Gravenhorst), 11  
*Atheta*, 9, 11  
 Audley-Charles, M.G., 76  
*austeni* Newstead, *Glossina*, 92–95, 100–101, 109, 111–117, 128  
*Austenina* Townsend, 90  
*Autalia*, 9  
 Autaliini, 12, 14–15  
 Axelrod, D.I., , 76  
     *see also* Raven, P.H., 75, 77–78, 80, 82  
*azteca*, *Ammophila*, 32  
 Badgley, M.E., , 9–10, 14  
     *see also* Moore, I., 9  
 Baldry, D.A.T., , 91, 103, 106  
     *see also* Burchard, R.P., 93  
 Ball, G.E., , 2  
     *see also* Erwin, T.L., 2, 4  
 Ball, I.R., 69  
 Barnes, W., 41  
*basilaris* Motschulsky, *Evarthrus*, 2  
 Baumgartner, H.,  
     *see* Dame, D.A., 111  
 Beaufort, L.F. de, 76  
 Beaver, R.A., 9  
 Benesh, B., 65  
 Berggren, W.A., 78  
 Bird, C.D., 40  
 Birkenmeyer, D.R.,  
     *see* Dame, D.A., 109  
     *see* Dean, G.J.W., 111–112  
 Biswas, B., 76  
 Blair, K.G., 10  
 Blum, M.S.,  
     *see* Brand, M., 13  
*Bolitochara*, 9  
 Bolitocharini, 12–15  
 Bolland, H.R., 96, 104  
*Boloria astarte*, 40  
*Bombyx*, 9  
 Bonin, J.,  
     *see* Dewey, J.F., 78  
 Borden, J.H.,  
     *see* Richerson, J.V., 25  
*Boreobia* Tschitschérine, 4  
 Boulger, G.S.,  
     *see* Britten, James, 38  
 Bourdoiseau, G.,  
     *see* Cuisance, D., 111  
 Brady, J.,  
     *see* Langley, P.A., 113  
 Brand, M., 13  
*Brasilucanus acomus* Ratcliffe, n. sp., 63, 65, 67  
*Brasilucanus alvarengai* Vulcano and Pereira, 62–63, 65, 83  
*Brasilucanus* Vulcano and Pereira, 65–68, 72, 76

- Brass, P., 8–10  
*brevipalpis* Newstead, *Glossina*, 96  
 Briden, J.C.,  
     *see* Smith, A.G., 75  
 Britten, James, 38  
 Bro Larsen, E., 10  
 Brown, F.M., 35, 37  
 Brown, K.S. Jr., 75  
*brucei* Plummer and Bradford,  
     *Trypanosoma*, 97, 102  
 Burchard, R.P., 93  
 Buren, A. van,  
     *see* Bolland, H.R., 96, 104  
 Burks, B.D.,  
     *see* Krombein, K.V., 27, 75  
 Bursell, E., 106–107, 114  
 Burt, E., 96  
 Buxton, P., 96  
 Callicerini, 12, 14–15  
 Camp, W.H., 75  
*Canarium*, 72  
*Caprinigidius trifurcatus* Didier, 66  
 Caraboidea, 350–447  
     Index to names of taxa, 448–464  
 Carlson, D.A.,  
     *see* Huyton, P.M., 116–117  
 Carne, P.B., 82  
 Casey, T.L., 2–4  
*castanea* Dejean, *Feronia*, 4  
*centralis* Machado, *Glossina*, 90, 92–95,  
     109, 111, 114, 116–119  
 Chadwick, P.R., 114  
 Chamberlin, J.S., 9  
 Chaudoir, M. de, 4  
*Chionobas chryxus* Doubleday, 35, 41–42  
*Chrysophyllum*, 72  
*chryxus* Doubleday, *Chionobas*, 35, 41–42  
*cicindeloides* (Schaller), *Stenus*, 10  
*Cinnamomum*, 72  
*Cissampelos*, 72  
 Claes, Y.,  
     *see* M'Pondi, A.M., 97, 102  
 Clair, M.,  
     *see* Cuisance, D., 111  
 Clarke, G.P.Y.,  
     *see also* Phelps, R.J., 98, 106  
 Clarke, J.E., 102  
 Clements, S.A.,  
     *see* Dean, G.J.W., 111–112  
*Clossiana astarte*, 35, 37–41  
 Coates, T.W., 114  
 Cobb, P.E.,  
     *see* Dame, D.A., 111  
*coerulescens* Gyllenhal, *Dianous*, 10  
 Colbert, E.H., 72  
 Cole, J.M., 40–41  
 Coleoptera, 10  
*Columbia*, 72  
 Conaghan, P.J.,  
     *see* Powell, C.M., 82  
*congolense* Broden, *Trypanosoma*, 97, 102  
*convivus* (LeConte), *Cyclotrachelus*, 2  
*convivus* LeConte, *Evarthrus*, 3  
 Cooke, H.B.S., 78  
*copricephalus* Deyrolle, *Penichrolucanus*,  
     62–63, 65, 68  
 Cornelissen, A.,  
     *see* Geest, L.P.S. van der, 98–100, 104,  
     106–108  
 Corner, R.G.,  
     *see* Schultz, C.B., 72  
 Corotocini, 12, 15  
 Coryndon, S.C., 79  
 Couvering, J.A. van,  
     *see* Berggren, W.A., 78  
 Cox, B.C., 72  
 Craig-Cameron, T.A., , 91, 94–95, 105  
     *see also* Pell, P.E., 91–92  
     *see also* Southern, D.I., 91–95,  
     117–118  
     *see* Curtis, C.F., 111  
 Cremastocheilini, 62  
*creusa* Doubleday, *Anthocharis*, 35, 41–42  
*Cryobius* Chaudoir, 2, 4  
*Cryptocarya*, 72  
 Csiki, E., 2, 4  
 Cuisance, D., 111  
 Curtis, C.F., , 111–119  
     *see also* Langley, P.A., 113  
*Cyclotrachelus* Chaudoir, 1–2  
*Cyclotrachelus convivus* (LeConte), 2  
*Cyclotrachelus roticollis* Casey, 2



- Cyclotrachelus s. str.*, 2, 4  
*Cyclotrachelus sigillatus* (Say), 3  
*Cyclotrachelus sodalis sodalis* (LeConte), 3  
*Cyclotrachelus torvus deceptus* Casey, 3  
*Cyclotrachelus torvus texanus* Motschulsky, 3  
D'Haeselfer, F.,  
    *see* M'Pondi, A.M., 97, 102  
Dame, D.A., , 109, 111, 114, 116  
    *see also* Dean, G.J.W., 111–112  
Darlington, P.J. Jr., 77  
Davidson, G., 111  
Davies, E.Ø.G., , 92–95  
    *see* Jordan, A.M., 93, 107  
Davis, D.M.,  
    *see* Heatwole, H., 25  
Davis, J.C., 97  
Dean, G.J.W., , 111–112  
    *see also* Dame, D.A., 114  
*decepta* Casey, *Eumolops*, 3  
Deinopsini, 10, 12–15  
Dewey, J.F., 78  
Deyrolle, H., 62  
*Dianous*, 11  
*Dianous coerulescens* Gyllenhal, 10  
Didier, R., 66  
Dietz, R.S., 77–78, 82  
*Diglotta*, 9, 14  
*Diglottini*, 14  
*Dinaraea*, 9, 11  
*disa mancinus*, *Erebia*, 35, 37–38, 41  
Distelmans, W., , 97, 102  
    *see also* M'Pondi, A.M., 97, 102  
*domestica* L., *Musca*, 52–54  
Dorf, E., 72  
Douglas, David, 39  
Dover, G., , 100  
    *see also* Amos, A., 91–92, 94, 100, 102  
Drepanoxenini, 15  
Drury, C.M., 39  
*Drusilla*, 9, 11, 14  
Duellman, W.E., 75  
Edwards, W.H., 37  
*elongatus* Arrow, *Penichrolucanus*, 62–63, 65, 67  
Elwes, H.J., 35  
*encelioides*, *Verbesina*, 32  
Endler, J.A., 75  
*Erebia disa*, 38  
*Erebia disa mancinus*, 35, 37–38, 41  
*Erebia mancinus* Doubleday, 35, 41–42  
Ermatinger, C.O., 39  
Erwin, T.L., 2, 4  
*et al.*, 32  
Etten, J. van, 98, 100, 103, 108  
*Euchloe creusa*, 35, 37–38, 40, 42  
*Eumolops decepta* Casey, 3  
*Eumolops impolita* Casey, 3  
*Euodynerus foraminatus* (Sauss.), 26–27  
Evans, A.M.,  
    *see* Newstead,, J.R., 90  
*Evarthrinus minax* Casey, 3  
*Evarthrus basilaris* Motschulsky, 2  
*Evarthrus convivus* LeConte, 3  
*Evarthrus* LeConte, 1–2, 4  
*Evarthrus licinoides* Motschulsky, 3  
*Evarthrus nimius* Motschulsky, 3  
*Evarthrus perseverus* Motschulsky, 2  
*Evarthrus s. str.*, 4  
*Evarthrus texanus* Motschulsky, 3–4  
Ewan, Joseph, 38  
*faber* Germar, *Molops*, 2  
*Falagria*, 9, 11  
Falagriini, 12, 14–15  
Fales, H.M.,  
    *see* Brand, M., 13  
Fauvel, A., 8–9  
*Feronia castanea* Dejean, 4  
*Feronia haematopus* Dejean, 4  
*Feronia imitatrix* Tschitschérine, 4  
*Feronia moesta* Say, 2  
*Feronia morio* Dejean, 2  
*Feronia nivalis* F. Sahlberg, 4  
*Feronia sigillata* Say, 2–3  
*Feronia sodalis* LeConte, 3  
*Feronia tenebricosa* Dejean, 2  
*Feronia valida* Dejean, 4  
Ferris, G.F.,  
    *see* Chamberlin, J.S., 9

- Fevrier, J.,  
     *see* Cuisance, D., 111
- Figulinae, 66
- Fleschner, C.A.,  
     *see* Badgeley, M.E., 9–10, 14
- Fletcher, James, 35
- foraminatus* (Sauss.), *Euodynerus*, 26–27
- Ford, H.R.,  
     *see* Dame, D.A., 114, 116
- Ford, J.,  
     *see* Dame, D.A., 114
- Forsyth, D.,  
     *see* Phillips, J.D., 78
- Fortax* Motschulsky, 2
- Frank, J.H., 11–12
- Freitag, R., 2–3
- Fuldner, D., 10
- fuscipes* Newstead, *Glossina*, 92–93, 95,  
     100, 105, 117–118
- gambiensis* Vanderplank, *Glossina*, 92–93,  
     108, 110
- Ganglbauer, L., 13, 98
- Gates, D.B.,  
     *see* Dame, D.A., 111
- Geest, L.P.S. van der, , 98–100, 104,  
     106–108  
     *see also* Bolland, H.R., 96, 104
- Gelechiidae, 27
- Georgevitsch, J., 11
- Geyh, M.A., 76
- Gillott, C., 115
- Glasgow, J.P., 90, 98
- Glossina austeni* Newstead, 92–95,  
     100–101, 109, 111–117, 128
- Glossina brevipalpis* Newstead, 96
- Glossina centralis* Machado, 90, 92–95,  
     109, 111, 114, 116–119
- Glossina fuscipes* Newstead, 92–93, 95,  
     100, 105, 117–118
- Glossina gambiensis* Vanderplank, 92–93,  
     108, 110
- Glossina martinii* Zumpt, 117–118
- Glossina morsitans* Westwood, 92–112,  
     114, 116–119
- Glossina pallidipes* Austen, 92–94,  
     100–104, 106–109, 112, 114–116, 124
- Glossina palpalis* Robineau-Desvoidy,  
     92–96, 106–107, 112, 114–115, 117
- Glossina s. str.*, 90
- Glossina submorsitans* Newstead, 92–94,  
     96, 106–109, 115
- Glossina submorsitans ugandensis*  
     Vanderplank, 117–118
- Glossina swynnertoni* Austen, 116–117
- Glossina tachinoides* Westwood, 92–93,  
     100, 103, 106, 108, 112, 117
- Glossina* Wiedemann, 90, 92
- Glover, R.G., 39–40
- Gooding, R.H., , 52–53, 95–101, 103–105,  
     107–110, 117, 119  
     *see also* Davis, J.C., 97  
     *see also* Distelmans, W., 97, 102  
     *see also* M'Pondi, A.M., 97, 102  
     *see also* Rolseth, B.M., 98–99, 105,  
         108–109
- Gose, W.A., 75
- Gunder, J.D., 42
- Gymnusini, 10, 12–15
- Gyrophæna*, 10
- Gyrophænina, 129–345  
     Index to names of taxa, 346–349
- Hackman, B.D., 77
- haematopus* Dejean, *Feronia*, 4
- Haffer, J., , 62, 75–76  
     *see* Simpson, B.B., 62, 75
- Hallam, A., 79
- Hamann, H.J., 112–113
- Hammond, P.M., 13
- Haploglossa*, 9
- Harley, J.M.B., 102
- Harris, C.R., 51
- Hartl, D.L., 54
- Heatwole, H., 25
- Helle, W.,  
     *see* Bolland, H.R., 96, 104  
     *see* Geest, L.P.S. van der, 98–100, 104,  
         106–108
- Hemming, Francis, 37
- Hennig, W., 65
- Hershkovitz, P., 75

- Hill, W.G.,  
     *see* Curtis, C.F., 111
- Hölldobler, B., 9–12
- Holden, J.C.,  
     *see* Dietz, R.S., 77–78, 82
- Hollebone, J.E.,  
     *see* Gooding, R.H., 98
- Holloway, B.A., 65
- Homalota*, 9
- Hooijier, D.A., , 76  
     *see also* Audley-Charles, M.G., 76
- Hoplandriini, 13
- House, A.P.R., 114
- Howard, R.W.,  
     *see* Kistner, D.H., 13–14
- Howden, H.F., 77
- Hulley, P.E., 91
- Hurd, P.D.,  
     *see* Krombein, K.V., 27
- Huyton, P.M., 116–117
- Hypherpes* Chaudoir, 4
- Hypocyphtinae, 13
- Hypocyphtini, 13–15
- imitatrix* Tschitschérine, *Feronia*, 4
- impolita* Casey, *Eumolops*, 3
- Itard, J., 91–93, 112–113
- Iwannek, K.H.,  
     *see* Hamann, H.J., 112–113
- Jackson, C.H.N., 117
- Jaenson, T.G.T., 103–104, 108, 115
- Jenkins, M.F., 10–12
- Johnson, D.L., 76–77
- Johnson, O.A., , 53–54  
     *see also* McDonald, I.C., 53
- Jones, G.,  
     *see* Veevers, J.J., 77
- Jordan, A.M., , 90, 93, 102, 107, 109–111, 115, 117  
     *see also* Dame, D.A., 109
- Jordan, K.H.C., 12
- Kasule, F.K., 11
- Kawooya, J., , 97, 116  
     *see also* Geest, L.P.S. van der, 98–100
- Keast, A., 75–77, 82
- Keleinikova, S.I., 3
- Kemner, N.A., 8–11, 13–14
- Kenchington, W., , 10  
     *see also* Rudall, K.M., 9
- Kirby, William, 39
- Kistner, D.H., , 12–14  
     *see also* Pasteels, J.M., 13–14  
     *see also* Shower, J.A., 12
- Klimaszewski, J., 13–14
- Kohler, Steve, 38
- Krombein, K.V., 27
- Kryger, J.P., 10
- Kudrass, H.R.,  
     *see* Geyh, M.A., 76
- Kuenen, P.H., 76
- Langley, P.A., , 90, 97, 113  
     *see also* Coates, T.W., 114  
     *see also* Curtis, C.F., 111, 113–114, 117, 119  
     *see also* Gillott, C., 115  
     *see also* Huyton, P.M., 116–117  
     *see also* Southern, D.I., 110–111  
     *see also* Tobe, S.S., 90
- Langley,, P.A.,  
     *see also* Curtis, C.F., 111–113, 117–119
- Laurent, R.F., 78
- Lavocat, R., 69
- Lawrence, J.F., 12
- Le Ray, D.,  
     *see* Distelmans, W., 97, 102  
     *see* M'Pondi, A.M., 97, 102
- Legner, E.F.,  
     *see* Moore, I., 9, 14
- Leopold, E.B., 72
- Leopold, R.A.,  
     *see* McDonald, I.C., 53  
     *see* Narang, S., 54
- Leptusa*, 8–10
- leverii* Arrow, *Penichrolucanus*, 62–63, 65–68, 77, 82
- licinoides* Motschulsky, *Evarthrus*, 3
- Livingstone, D.A., 75, 78
- Lloyd, J.J., 75
- Lohse, G.A., 13
- Lomechusa*, 9, 12
- Lomechusoides*, 9, 12
- Lucanidae, 65–67, 72

- luctosa*, *Podalonia*, 31–32  
*Lucuma*, 72  
 Lynch, J.D., 75  
 M'Pondi, A.M., , 97, 102  
     *see also* Distelmans, W., 97, 102  
 MacGinitie, H.D., , 72  
     *see also* Leopold, E.B., 72  
 MacGregor, J.G., 39  
 MacKelvey, S.D., 39–40  
 Macleod, M.A., 39  
*mancinus* Doubleday, *Erebia*, 35, 41–42  
 Mannerheim, C.G., 4  
 Martin, L.D.,  
     *see* Schultz, C.B., 72  
*martinii* Zumpt, *Glossina*, 117–118  
 Maschwitz, U.,  
     *see* Hölldobler, B., 9  
*Mastixia*, 72  
 Matolin, S., 114  
 Maudlin, I., 91, 94–96, 102, 107, 117  
 McDonald, I.C., , 53–54  
     *see also* Narang, S., 54  
 McDunnough, J.H.,  
     *see* Barnes, W., 41  
 Medway, L., 76  
 Meijer, W., 76–77  
*Meliosma*, 72  
*Melitaea anicia* Doubleday, 35, 41–42  
 Metzler, M.,  
     *see* Peschke, K., 13  
 Mews, A.R.,  
     *see* Curtis, C.F., 111–113  
 Miller, L.D., 37  
*minax* Casey, *Evarthrinus*, 3  
 Möglich, M.,  
     *see* Hölldobler, B., 9  
*moesta* Say, *Feronia*, 2  
*moestus* (Say), *Pterostichus*, 2  
*Molops faber* Germar, 2  
*Monarda pectinata*, 32  
 Moore, B.P., 65  
 Moore, I., 9, 14, 91  
*morio* Dejean, *Feronia*, 2  
*mormonia* (Bdv.), *Speyeria*, 35  
*morsitans* Westwood, *Glossina*, 92–112,  
     114, 116–119  
 Motschulsky, V. von, 3  
 Mtuya, A.G.,  
     *see* Dame, D.A., 111  
 Müller, P., 75  
*Musca domestica* L., 52–54  
 Myllaenini, 10, 12–15  
 Myrmedoniini, 12–15  
 Narang, S., 54  
 Nash, T.A.M., , 106  
     *see also* Dame, D.A., 109  
     *see also* Jordan, A.M., 109  
 Nei, M., 107  
*Nemorhina* Robineau-Desvoidy, 90  
*Neolitsea*, 72  
 Neuroptera, 10  
 Newstead, J.R., 90  
 Newton, A.F.,  
     *see* Lawrence, J.F., 12  
*nicobaricus* Arrow, *Penichrolucanus*,  
     62–63, 65–66, 68  
*nimius* Motschulsky, *Evarthrus*, 3  
*nivalis* F. Sahlberg, *Feronia*, 4  
*Occidryas anicia*, 35, 37–38, 41  
 Oecophoridae, 27  
*Oeneis chryxus*, 35, 37–38  
 Offori, E.D.,  
     *see* Curtis, C.F., 111–113  
 Olethreutidae, 27  
*Oligota*, 9–10, 14  
 Oligotini, 12–15  
 Opler, P.A., 37–38, 40  
 Ormsby, M.A., 40–41  
 Overland, D.E.,  
     *see* McDonald, I.C., 54  
 Oxypodini, 12–15  
 Paederinae, 11  
*pallidipes* Austen, *Glossina*, 92–94,  
     100–104, 106–109, 112, 114–116, 124  
*palpalis* Robineau-Desvoidy, *Glossina*,  
     92–96, 106–107, 112, 114–115, 117  
*parkeri*, *Prionyx*, 31  
*Parnassius*, 41  
*Parnassius phoebus smintheus*, 35, 37–41  
*Parnassius smintheus* Doubleday, 35, 41  
 Pasteels, J.M., , 12–14  
     *see also* Brand, M., 13

- Paulian, R., 9, 11  
 paussine Carabidae, 62  
*pectinata*, *Monarda*, 32  
 Pell, P.E., , 91–93, 95, 105  
     *see also* Craig-Cameron, T.A., 91, 94–95, 105  
     *see also* Curtis, C.F., 95, 111–113  
     *see also* Southern, D.I., 91–96, 106–107, 110–111, 117–118  
     *see* Jordan, A.M., 93, 107  
*Pella*, 9  
 Penichrolucaninae, 61–62, 65–67, 69, 72, 75–78, 80, 82  
*Penichrolucanus copricephalus* Deyrolle, 62–63, 65, 68  
*Penichrolucanus* Deyrolle, 62, 65–68, 82  
*Penichrolucanus elongatus* Arrow, 62–63, 65, 67  
*Penichrolucanus leveri* Arrow, 62–63, 65–68, 77, 82  
*Penichrolucanus nicobaricus* Arrow, 62–63, 65–66, 68  
*Penichrolucanus sumatrensis* Arrow, 62–63, 65–66, 68  
 Pereira, F.S.,  
     *see* Vulcano, M.A., 62–63  
 Perissodactyla, 72  
 Perris, E., 8  
*perseverus* Motschulsky, *Evarthrus*, 2  
 Peschke, K., 10, 13  
 Peyerimhoff, P. de, 11  
 Phelps, R.J., 98, 106  
*Pheryphes* Casey, 4  
 Phillips, J.D., 78  
*Phloeopora*, 8, 14  
*phoebeus smintheus*, *Parnassius*, 35, 37–41  
*Phytocrene*, 72  
 Phytosini, 12–15  
 Pike, E.M., 37, 40–41  
 Pinhão, R.C., 115  
 Pitman, W.C. III, , 78  
     *see also* Dewey, J.F., 78  
*Placusa*, 9, 14  
*Platysma amethystinum*, 4  
*Podalonia luctosa*, 31–32  
*Podalonia valida* (Cresson), 32  
*Poecilus* Bonelli, 4  
 Politzar, H.,  
     *see* Cuisance, D., 111  
 Potts, W.H., , 90, 111, 117  
     *see also* Newstead, J.R., 90  
 Powell, C.M., 82  
 Prance, G.T., 75–76  
*Prionyx parkeri*, 31  
*procerus* (Gravenhorst), *Astenus*, 11  
 Pronomacini, 10, 12–15  
*Pseudocryobius* Motschulsky, 4  
 Pterostichini, 1, 4  
*Pterostichus (Poecilus) texanus* LeConte, 4  
*Pterostichus algidus* LeConte, 4  
*Pterostichus* Bonelli, 2, 4  
*Pterostichus moestus* (Say), 2  
*Pterostichus tarsalis* LeConte, 4  
*Pterostichus texicola* Csiki, 4  
 Pyralidinae, 27  
 Pyraustinae, 27  
 Quantin, P., 77  
 Radinsky, L., 72  
 Raven, P.H., 75–78, 80, 82  
 Rey, C., 8  
 Richerson, J.V., 25  
 Riordan, K., 91, 93  
 Robinson, A.S.,  
     *see* Curtis, C.F., 111  
 Rogers, A., 115–116  
 Rolseth, B.M., , 98–99, 105, 108–109  
     *see also* Gooding, R.H., 52, 97–101, 104–105, 107–108, 110  
 Romer, A.S., 72  
 Roon, G. van, 66, 72  
*roticollis* Casey, *Cyclotrachelus*, 2  
 Rudall, K.M., 9  
 Ryan, W.B.F.,  
     *see* Dewey, J.F., 78  
 Sartono, S., 76  
 Savage, R.J.G.,  
     *see* Coryndon, S.C., 79  
 Scarabaeidae, 62  
 Schlick, W., 10  
 Schmidt, C.H., 111  
 Schultz, C.B., 72

- Schuster, R.M., 76  
 Schwarz, M.,  
   *see* Huyton, P.M., 116–117  
 Scott, G.R.,  
   *see* Gose, W.A., 75  
 Séguy, E.,  
   *see* Didier, R., 66  
 Seevers, C.H., 13–14  
 Sellin, E.,  
   *see* Cuisance, D., 111  
 Service, M.W., 119  
 Shepard, P.M.,  
   *see* Brown, Jr., K.S., 75  
 Shircore, J.O., 96  
 Shower, J.A., 12  
*sigillata* Say, *Feronia*, 2–3  
*sigillatus* (Say), *Cyclotrachelus*, 3  
 Silvestri, f., 9  
 Simpson, B.B., 62, 75  
*smintheus* Doubleday, *Parnassius*, 35, 41  
 Smith, A.G., 75, 78  
 Smith, D.R.,  
   *see* Krombein, K.V., 27  
*sodalis* (LeConte), *Cyclotrachelus*  
   *sodalis*, 3  
*sodalis* LeConte, *Feronia*, 3  
 Soper, J.D., 39  
 Southern, D.I., , 91–96, 106–107,  
   110–111, 114, 117–118  
   *see also* Craig-Cameron, T.A., 91,  
     94–95, 105  
   *see also* Curtis, C.F., 111–113  
   *see also* Davies, E.D.G., 92–95  
   *see also* Jordan, A.M., 93, 107  
   *see also* Pell, P.E., 91–93, 95, 105  
*Speyeria mormonia* (Bdv.), 35  
 Spradbery, J.P., 25  
 Staphylinidae, 8  
 Steiner, A.L., 26–27, 31–32  
 Steninae, 11  
*Stenus*, 10–11  
*Stenus cicindeloides* (Schaller), . . .  
*Stereocerus* Kirby, 4  
 Strecker, Herman, 35  
 Streif, H.,  
   *see* Geyh, M.A., 76  
*submorsitans* Newstead, *Glossina*, 92–94,  
   96, 106–109, 115  
*submorsitans ugandensis* Vanderplank,  
   *Glossina*, 117–118  
*sumatrensis* Arrow, *Penichrolucanus*,  
   62–63, 65–66, 68  
 Surgeoner, G.A.,  
   *see* Harris, C.R., 51  
 Swartz, D.K.,  
   *see* Gose, W.W., 75  
*swynnertoni* Austen, *Glossina*, 116–117  
*Symplocos*, 72  
*tachinoides* Westwood, *Glossina*, 92–93,  
   100, 103, 106, 108, 112, 117  
 Takeuchi, T.,  
   *see* Agatsuma, T., 54  
 Talent, J.A.,  
   *see* Veevers, J.J., 77  
 Talwani, M.,  
   *see* Pitman III, W.C., 78  
 Tapiridae, 75  
 Tarling, D.H., 77–78  
*tarsalis* LeConte, *Pterostichus*, 4  
 Taze, Y.,  
   *see* Cuisance, D., 111  
*tenebricosa* Dejean, *Feronia*, 2  
*Terminalia*, 72  
 Termitohospitini, 12  
 Termitonannini, 12  
*Termitoptochus*, 9  
 Terranova, A.C.,  
   *see* McDonald, I.C., 53  
   *see* Narang, S., 54  
*texanus* LeConte, *Pterostichus* (*Poecilus*),  
   4  
*texanus* Motschulsky, *Evarthrus*, 3–4  
*texicola* Csiki, *Pterostichus*, 4  
*Thamiaraea*, 9, 11  
 Thompson, R.G., 2  
 Tjon-a-joe, H.P.,  
   *see* Geest, L.P.S. van der, 98–100, 104,  
     106–108  
 Tobe, S.S., 90  
 Tortricidae, 27

- torvus deceptus* Casey, *Cyclotrachelus*, 3  
*torvus texanus* Motschulsky,  
     *Cyclotrachelus*, 3  
 Townes, H.K., 26  
 Trewern, M.A.,  
     *see* Curtis, C.F., 117–119  
     *see* Jordan, A.M., 93, 107, 109  
 Tricart, J., 75  
 Trichopseniinae, 10, 13–14  
 Trichopseniini, 13  
*trifurcatus* Didier, *Caprinigidius*, 66  
*Trypanosoma brucei* Plummer and  
     Bradford, 97, 102  
*Trypanosoma congolense* Broden, 97, 102  
 Turnbull, S.A.,  
     *see* Harris, C.R., 51  
 Turner, J.R.G.,  
     *see* Brown, Jr., K.S., 75  
 Umbgrove, J.H.F., 76  
*valida* (Cresson), *Podalonia*, 32  
*valida* Dejean, *Feronia*, 4  
 Vanderplank, F.L., 90, 95–96, 116–119  
 Veevers, J.J., 77  
 Velthuis, H.H.W., 54  
*Verbesina encelioides*, 32  
 Verhoeff, K.W., 8–12  
 Verstappen, H.Y., 76  
 Vloedt, A.M.V. van der, , 96–97, 107, 116  
     *see* Matolin, S., 114  
 Vuilleumier, B.S., 62, 75  
 Vulcano, M.A., 62–63  
 Walker, D., 76  
 Warner, P.V.,  
     *see* Dame, D.A., 111  
 Warren, E., 10  
 Wasmann, E., 9–10  
 Watrous, L.E., 66  
 Weinreich, E., 10–11  
 Welch, R.C., 10  
 Wenner, A.M.,  
     *see* Heatwole, H., 25  
 Westwood, J.O., 35  
 Wheeler, Q.D.,  
     *see* Watrous, L.E., 66  
 Whistlecraft, J.W.,  
     *see* Harris, C.R., 51  
 White, James,  
     *see* Ermatinger, C.O., 39  
 Whitehead, D.R.,  
     *see* Erwin, T.L., 2, 4  
 Williamson, D.L.,  
     *see* Dame, D.A., 111  
 Woodring, W.P., 75  
 Wortham, S.M.,  
     *see* Dean, G.J., 111–112





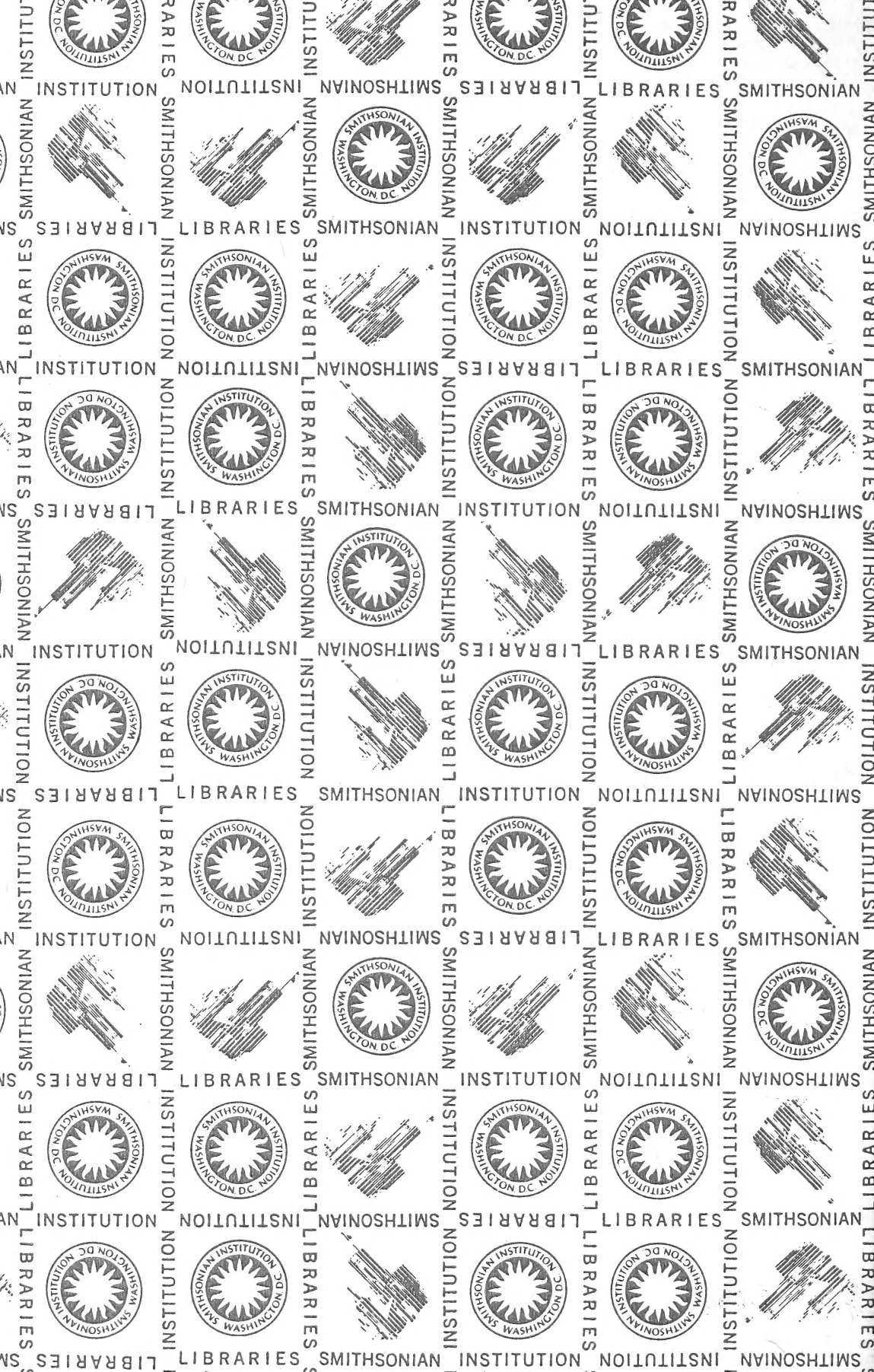


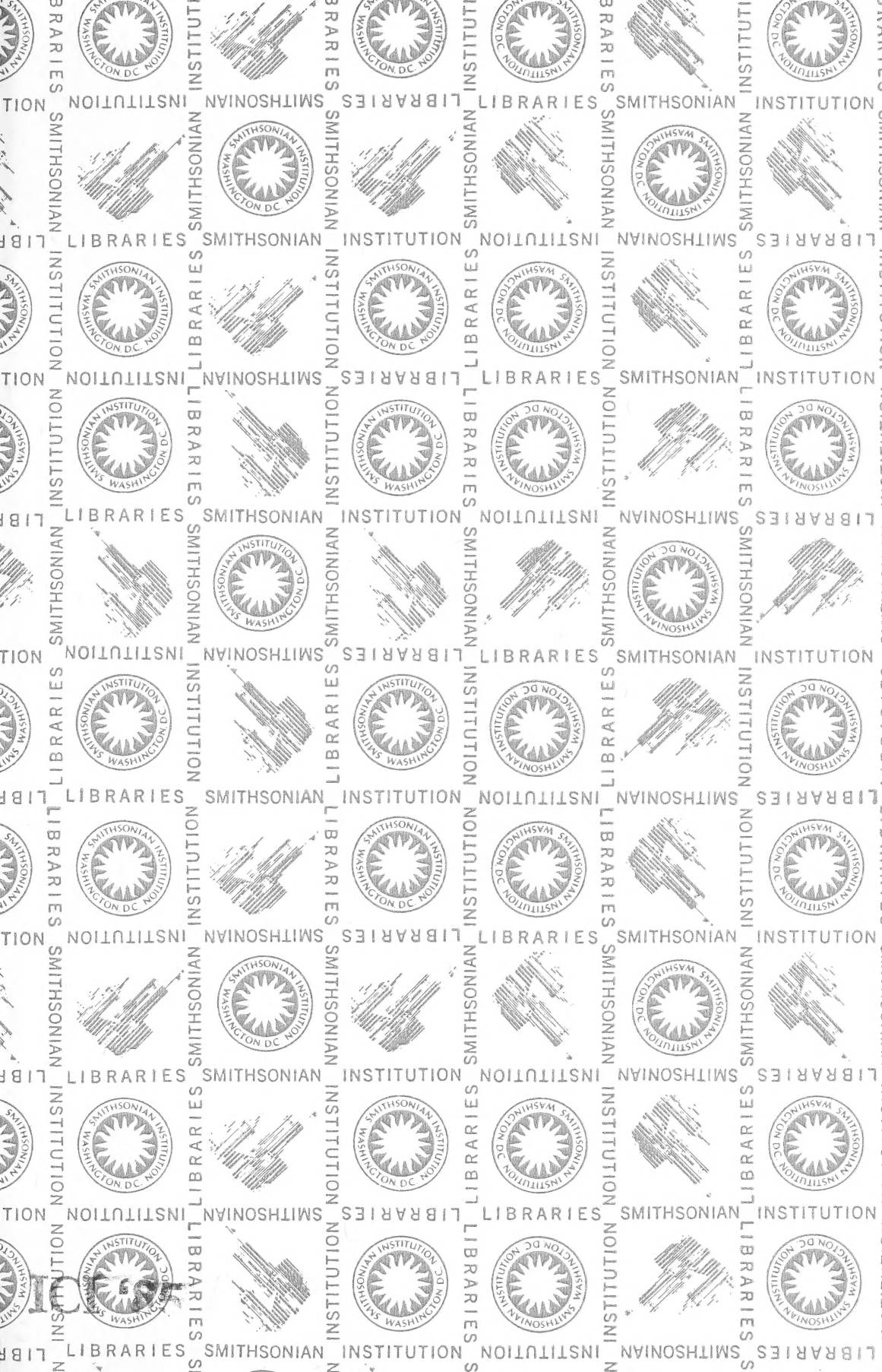












SMITHSONIAN INSTITUTION LIBRARIES



3 9088 00908 7628